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THE UNIVERSITY OF ALBERTA

A STUDY OF LOW CHLOROPHYLL LEVELS RELATIVE TO HIGH PHOSPHORUS AND NITROGEN LEVELS IN PRAIRIE SALINE LAKES

by

© Christine E. Campbell

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF

MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1986

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ISBN 0-315-30138-4

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DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE

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PERMANENT ADDRESS:

S7 Cpt 35
RR#3 Argue Drive
Westbank, British Columbia

DATED November 14, 1985

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FACULTY OF GRADUATE STUDIES AND RESEARCH

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E E Prepas
.....
Supervisor

M. Hickman
.....

A R Pal
.....

W C Mackay
.....

J Lebst Les
.....

DATE Nov 26 1985

Abstract

Prairie saline lakes are extremely unproductive: chlorophyll *a* (Chl*a* - a measure of algal biomass) levels are low despite extraordinarily high concentrations of total phosphorus (TP) and total nitrogen (TN). To evaluate why these saline systems are so unproductive relative to freshwater systems, three saline lakes (Fluevog, Peninsula and Oliva Lakes; total dissolved solids > 5000 $mg \cdot L^{-1}$) in eastern Alberta were studied intensively in 1983 and 1984 with a modification of analytical techniques developed for freshwater systems. Oliva Lake exhibited marked inverse chemical and thermal stratification over the summer; both Fluevog and Peninsula Lakes remained unstratified throughout the year. In these three lakes, mean summer phytoplankton Chl*a* ranged from 3 to 10 $ug \cdot L^{-1}$, mean summer phytobenthos Chl*a* was less than 70 $mg \cdot m^{-2}$, while mean summer TP and TN ranged from 2000 to 13000 and from 4000 to 11000 $ug \cdot L^{-1}$, respectively. Measured phytoplankton and phytobenthos Chl*a* and phytoplankton primary production were extremely low relative to values predicted from measured TP and TN levels and empirical models developed for fresh waters. Thus, neither the phytoplankton nor phytobenthos communities were efficiently using the high nutrient levels in the lakes. Although algal bioassays with $^{32}P\text{-}PO_4$ and KH_2PO_4 indicated that phosphorus was not limiting to algal growth in the lakes, bioassays with KNO_3, NH_4Cl and EDTA suggested that inorganic nitrogen was in demand in all the lakes and that iron was in demand in Oliva Lake. Bacteria densities and zooplankton dry weight were remarkably high (> 10^7 $cells \cdot mL^{-1}$ and > 1.0 $mg \cdot L^{-1}$, respectively) in the study lakes relative to values predicted from Chl*a* and phytoplankton biomass levels and empirical models from freshwater systems. Phytoplankton biomass in the lakes was insufficient to support zooplankton population growth; bacteria and detritus were likely a major zooplankton food source.

This study suggests that empirical freshwater models that predict Chl*a* and primary productivity from TP and TN levels, as well as bacteria density and zooplankton biomass from Chl*a* and phytoplankton biomass levels, are not applicable in prairie saline lakes. In contrast to

many freshwater lakes, TP does not limit algal growth and TN does not appear to be a good estimate of biologically available nitrogen in the saline lakes. The water budgets suggest that phosphorus behaves as a conservative element in the study lakes. Cycling of organic matter in the saline lakes also differs from those in freshwater lakes since bacteria and detritus, rather than phytoplankton, appear to be the major source of food for zooplankton. However, high salinity and concentrations of specific ions, rather than high zooplankton and bacteria populations, seem to be most important in limiting algal growth in the prairie saline lakes.

Acknowledgements

I would like to thank my supervisor, Dr. E. Prepas, for her interest and support for this study. The members of my committee, Dr. M. Hickman, Dr. J. Holmes and Dr. W. Mackay, also provided useful advice. Ms. J. Bierhuizen, Dr. H. Fricker, Dr. P. Gorham, Ms. N. Munn and Dr. A. Trimbee gave many helpful suggestions. Ms. N. Munn and Dr. A. Trimbee reviewed parts of this manuscript.

My two summer assistants, Ms. I. Wisheu in 1983 and Ms. A. Opazo in 1984, provided invaluable aid in both field and laboratory; their muscle power contributed immensely to this study. Other adventurous souls who helped me in the field were Mr. J. Babin, Ms. J. Bierhuizen, Mr. B. Lei, Mr. J. Mckague, Ms. N. Munn, Ms. J. Newcomb, Ms. F. Parkinson and Mr. S. So. Both Ms. G. Hutchinson and Ms. J. Vickery uncomplainingly helped me to find my way around the laboratory.

Special thanks go to Mr. Thorcuill MacDonald and others at the University of Alberta Beef Cattle Ranch in Kinsella, Alberta for allowing me to set up a trailer on the ranch, and to the Department of Zoology at the University of Alberta for providing me with the trailer. Sincere thanks are also due to the Fluevog family at Fluevog Lake and the Cameron family at Peninsula Lake who allowed me to dock boats on their property. The Hunter family at Oliva Lake kindly allowed me the use of their boat, as well.

Dr. P. Gorham and Ms. J. Shamess aided in the identification of phytoplankton species, Dr. D. Allen aided in phytobenthos identification, Mr. B. Husband aided in macrophyte identification and Dr. A. Salki (Freshwater Institute, Winnipeg) confirmed my zooplankton identifications. Mr. D. Bird (McGill University) was instrumental in undertaking bacteria counts. Mr. Blawacky and others at the University of Alberta Botany Department provided use of the scintillation counter. Both Dr. V.H. Smith and Dr. A. Trimbee kindly provided unpublished data.

Financial support was provided by a Boreal Institute Grant-in-Aid for Northern Research to Ms. C. Campbell as well as research grants from the National Science and Engineering Research Council and Canadian National Sportsmen's Fund to Dr. E. Prepas.

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I. General Introduction

Inland saline lakes are a common but little studied phenomenon of the landscape of western Canada. Saline lakes are found from southern Manitoba through to central Alberta (Rawson and Moore 1944; Driver and Peden 1977; Barica 1978; Bierhuizen and Prepas 1985) and in the dry Interior of British Columbia (Northcote and Larkin 1956; Scudder 1969; Blinn 1971). In these regions, lake evapotranspiration rates exceed atmospheric precipitation rates and thus there is concentration of dissolved salts in many lake basins. These saline lakes are important as nesting and feeding areas for migratory waterfowl and as potential sites for sports fisheries and recreation. In view of the varied demands on saline lakes, a Workshop on Prairie Lake Restoration (National Water Research Institute, Winnipeg, October 1983) indicated that the study of factors controlling productivity in these lakes was of prime importance to the management and scientific understanding of inland saline lakes in western Canada.

Globally, there is no clear chemical definition of a saline lake. Saline lakes have been defined as those lakes with levels of total dissolved solids (TDS) that range from $>$ 300 to 500 $mg\text{-}L^{-1}$ (Rawson and Moore 1944; Northcote and Larkin 1963) to $>$ 3000 $mg\text{-}L^{-1}$ (Williams 1964; Bayly 1967) or even $>$ 5000 $mg\text{-}L^{-1}$ (Beadle 1981). These definitions of salinity are determined mainly by a "brackish taste" of the water and thus are fairly arbitrary from a biological standpoint. The physiological barriers that prevent a given freshwater species from living in water above a certain salinity are largely unknown, although most of the organisms that are considered freshwater species are naturally found in waters with TDS $<$ 1000 $mg\text{-}L^{-1}$ (Beadle 1969). Consequently, saline lakes may be most adequately defined by biological criteria to have TDS $>$ 1000 $mg\text{-}L^{-1}$. However, definitions of salinity that are based on TDS levels do not give any information on the ionic composition of the water. Ionic composition and salinity levels can vary a great deal between lakes, even within the same physiographic area (Barica 1975). Freshwater lakes can often be located within a few km of highly saline lakes (Binyon 1952).

Elevated levels of phosphorus are characteristic of many inland saline lakes (Hutchinson 1937). These lakes are often situated in closed basins at the terminal end of a drainage system and thus serve as nutrient and ion sinks.

Many broad similarities exist between saline lake communities throughout the world. Most saline lakes are simple ecosystems with low species diversity that results from the physiological constraints of salinity (Williams 1972). In general, when TDS > 1000 mg-L^{-1}, the algal community is dominated by blue-green algae and diatoms with some green algae (Cole 1968; Hammer et al. 1983). Benthic algae (phytobenthos) populations are common in some shallow saline lakes with rocky substrates (Castenholz 1960; Wetzel 1964). Macrophytes are rare in saline lakes with TDS > 8000 mg-L^{-1} (Rawson and Moore 1944). High salinity levels may limit the ability of macrophytes to produce cell walls that are sufficiently thick to limit injurious salt uptake (Weirich 1974). Pelagic bacteria, primarily chemosynthetic species, can be very abundant in inland saline lakes (i.e. densities up to 10^9 cells-mL^{-1} as recorded by Mason 1967; Kaplan and Friedman 1970; Walker 1975; Cohen et al. 1977; Kilham 1981) and often reach densities that are a hundred times those reported for freshwater lakes. Populations of chemosynthetic bacteria (such as nitrifying and sulfur-oxidizing species) and photosynthetic bacteria (such as pigmented sulfur-reducing species) are especially common at the chemocline in meromictic saline lakes (as recorded by Culver and Brunskill 1969; Axler et al. 1978; Cloern et al. 1978; Lawrence et al. 1978; Hamilton-Galat and Galat 1983; Northcote and Hall 1983). In shallow and highly saline lakes (TDS > 10,000 mg-L^{-1}), large microbial populations are often associated with blue-green algae in benthic mats (Bauld 1981; Jorgensen et al. 1983). Zooplankton and benthic fauna diversity is low in saline lakes (Rawson and Moore 1944; Edmondson 1963) with often only a few species present, such as the brine shrimp, ***Artemia salina***. Fish are generally absent from saline lakes with TDS > 10,000 mg-L^{-1} (Rawson and Moore 1944) since the majority of freshwater fish species are unable to withstand the high osmotic pressures (reviewed by Machniak 1977). Even if fish are present at high salinities, they might not be able to reproduce there (Hammer et al. 1975). Few fish species are adapted to

salinities > 10,000 mg-L^{-1} TDS; examples are the Lahontan cut-throat trout *Salmo clarki henshawi*, native to saline Pyramid lake, Nevada (Taylor 1972), and various cyprinodont fishes (Beadle 1943; Barlow 1958).

Salinity levels can vary greatly over time in inland saline lakes due to lake evaporation and dilution (Bayly and Williams 1966; Cole 1968). In terms of the species composition in the lakes, the ability of organisms to be *euryhaline* (able to adapt to a wide range of salinities) is often more important than the ability to simply tolerate high salinity levels.

Although there are broad similarities between saline lake communities, levels of algal production can vary immensely among lakes in different regions. Inland saline lakes in western Canada are generally unproductive with low levels of phytoplankton chlorophyll *a* - a measure of algal biomass. In central Alberta, chlorophyll *a* levels less than 3 *u*g-L^{-1} (oligotrophic according to Wetzel 1983) have been reported for some saline lakes despite levels of total phosphorus and total nitrogen greater than 2000 *u*g-L^{-1} (Bierhuizen and Prepas 1985). Chlorophyll *a* levels decreased significantly as salinity increased in 18 Alberta saline lakes (Bierhuizen and Prepas 1985). Although studies on saline lakes in Manitoba (Barica 1978) did not show any significant relationships between chlorophyll *a* and specific conductivity (a measure of salinity with a rough 1:1 linear relationship with TDS at TDS < 300,000 mg-L^{-1}; Williams 1966), algal blooms were limited to lakes with conductivity < 3000 *u*mhos-cm^{-1}. In the saline lakes in Saskatchewan studied by Haynes and Hammer (1978) and Hammer (1978), chlorophyll *a* levels and primary production rates generally decreased to less than 3 *u*g-L^{-1} and 300 mgC-m^{-2}-d^{-1}, respectively, as TDS increased above 5000 mg-L^{-1}, even though total phosphorus levels ranged from 200 to 2000 *u*g-L^{-1}. (My analysis of their data shows a negative correlation between primary production and salinity: $r^2 = 0.42$, $P < 0.001$; $n = 7$. Insufficient data were available for a statistical analysis of chlorophyll and salinity levels in the Saskatchewan lakes). Saline lakes in British Columbia (Topping 1975) also exhibited decreased phytoplankton production when TDS increased above 1000 mg-L^{-1}, although the relationship between salinity and algal production was not quantified.

In contrast to these mainly unproductive saline lakes in western Canada, studies on saline lakes in Australia (Hammer 1981), Egypt (Aleem and Samaan 1969), East Africa (Melack and Kilham 1974) and the western U.S. (Armstrong et al. 1966; Walker 1975; Stephens and Gillespie 1976) reported very productive systems with chlorophyll *a* levels from 10 to 500 $ug\text{-}L^{-1}$ and rates of primary production greater than 1000 mg $C\text{-}m^{-2}\text{-}d^{-1}$ (eutrophic according to Wetzel 1983) along with total phosphorus and total nitrogen levels from 200 to over 2000 $ug\text{-}L^{-1}$. However, factors responsible for the differences in productivity levels between saline lakes in various regions have yet to be investigated.

Prairie saline lakes in central Alberta are therefore extraordinarily unproductive given their high nutrient levels. In this study, three saline lakes in central Alberta with TDS > 5000 $mg\text{-}L^{-1}$ were investigated intensively to determine the possible factors responsible for the low levels of phytoplankton chlorophyll *a*, and to determine if phytoplankton chlorophyll *a* is a good estimate of primary productivity in prairie saline lakes (i.e. there is no unusually rapid algal turnover rates). Phytoplankton growth and chlorophyll levels can be limited by a number of chemical and biological interactions. High levels of TDS or specific ions in the study lakes could depress phytoplankton growth by osmotic stress (Por 1980). Measured TP and TN levels might not be good estimates of biologically available phosphorus and nitrogen in the saline lakes, in contrast to freshwater lakes (Smith 1982); phosphorus or nitrogen would thus be limiting to phytoplankton growth as reported in saline lake studies by Stephens and Gillespie (1976) and Moss (1969). Necessary trace elements such as iron could be in short supply as observed in saline Devil's Lake, North Dakota (Shubert 1978). The phytoplankton community in the study lakes might also be out-competed for available nutrients by large communities of phytobenthos (reported from saline Borax Lake, California; Wetzel 1964) and pelagic bacteria (reported from saline lakes in East Africa; Kilham 1981). Unusually large zooplankton communities in the lakes could heavily crop the phytoplankton chlorophyll, as Anderson (1958) suggested for saline Soap Lake, Washington. Such interactions then, either singly or in combination, might have important effects on phytoplankton productivity in prairie saline

lakes.

From this study, a picture emerges of inland saline lakes as unique ecosystems in western Canada. Due to their importance in the prairie biome and their increasing economic importance, inland saline lakes deserve further scientific study.

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II. Evaluation of factors related to the unusually low chlorophyll levels in prairie saline lakes

A. Introduction

While inland saline lakes (total dissolved solids - TDS > 1000 mg-L^{-1}) in many areas of the world often have high phytoplankton chlorophyll *a* (Chl*a*) levels (review of saline lake studies in Africa, Australia and western U.S.A.; Hammer 1981), such high Chl*a* levels are uncommon in prairie saline lakes in western Canada. Saline lakes in central Alberta (Bierhuizen and Prepas 1985) often exhibit unusually low Chl*a* levels (< 10 *u*g-L^{-1}) relative to extraordinarily high total phosphorus (TP) and total nitrogen (TN) levels (> 2000 *u*g-L^{-1}). Chl*a* decreased significantly as salinity increased in the 18 Alberta saline lakes studied by Bierhuizen and Prepas. Low Chl*a* levels have been reported for other saline lakes in western Canada such as in Manitoba (Barica 1978), Saskatchewan (Haynes and Hammer 1978) and in the dry interior of British Columbia (Topping 1975), although the relationship between Chl*a* and salinity levels was not quantified. Low Chl*a* levels thus appear to be a distinct characteristic of prairie saline lakes.

Several hypotheses could explain the low Chl*a* levels in the saline lakes on the Canadian prairies:

1. Phytobenthos rather than phytoplankton is the dominant primary producer in these generally shallow saline systems, as Wetzel (1964) found in Borax Lake, California.

2. Phytoplankton Chl*a* is not a good estimate of productivity in saline lakes due to unusually rapid algal turnover rates.

3. Biologically available phosphorus, nitrogen and iron levels are sufficiently low to dramatically limit algal growth, as reported in some saline lake studies (inorganic nitrogen limitation by Stephens and Gillespie 1976; iron and inorganic nitrogen limitation by Shubert 1978; phosphorus and inorganic nitrogen limitation by Moss 1969).

4. Extremely high densities of pelagic bacteria, similar to those reported for saline lakes in East Africa by Kilham (1981), are diverting nutrients from the phytoplankton.

5. High zooplankton populations are cropping the phytoplankton Chl*a* at unusually high rates, as Anderson (1958) suggested for saline Soap Lake, Washington.

To test these five hypotheses, three saline lakes in central Alberta (Fluevog, Peninsula and Oliva lakes; TDS > 5000 mg-L^{-1}) were studied from April 1983 to September 1984. Phytobenthos Chl*a* was measured to determine its relative importance to total algal biomass. Phytoplankton Chl*a* and primary productivity were monitored to evaluate whether phytoplankton Chl*a* was a good estimate of primary production and to determine the relationship of these parameters to measured TP and TN levels. Phosphorus limitation was tested by ^{32}P-PO_4 uptake experiments on freshly collected lake water and by the addition of KH_2PO_4 to laboratory bioassays. Nitrogen, iron and general nutrient limitation were tested by bioassay additions of NH_4Cl and KNO_3, iron chelate EDTA, and soil extract solution (SE), respectively. To estimate bacterial abundance and the relative contribution of bacteria to secondary zooplankton production (on the assumption that the majority of bacteria were autotrophic as is true for other saline lakes, e.g. Kaplan and Friedman 1970 and Cohen et al. 1977), pelagic bacteria populations were enumerated. To evaluate the impact of zooplankton grazing, zooplankton dry weight and population numbers were monitored and compared to phytoplankton biomass. The data collected on the three saline lakes were then compared with empirical models developed for freshwater lakes.

B. Methods

Field collection

The three study lakes were chosen on the basis of their wide range of salinities, phytoplankton Chl*a* levels (Bierhuizen and Prepas 1985) and accessibility. Biweekly visits were made to each lake from April to September 1983 and 1984, and monthly visits were made over the winter of 1983. On each visit, vertical profiles of temperature were measured at a main station defined as the deepest site in the lake. Similar vertical profiles of specific conductivity (a measure of salinity roughly comparable with TDS; Williams 1966) were measured in 1984. Both conductivity and temperature were determined at 0.5-m intervals in Fluevog and

Peninsula Lakes and at 0.25-m intervals in Oliva Lake from the surface to within 0.25 m from the lake bottom with a Hydrolab TC-2 metre. The trophogenic zone was defined as twice Secchi depth in Fluevog and Peninsula Lakes. In Oliva Lake, as Secchi depth equalled maximum lake depth, the trophogenic zone was defined to within 0.5 m of the lake bottom to avoid collection of bottom sediment in water samples from the trophogenic zone. During ice free periods, changes in lake volume were estimated by changes in water level recorded on a permanent marker in each lake. The lakes were hand sounded in August 1983 to determine basin morphometry. Surface areas of the lakes were determined from 1:50,000 topographic maps and 1:5000 aerial photographs. Drainage basin areas were determined from 1:50,000 topographic maps.

Water samples for analysis of phosphorus, nitrogen and phytoplankton Chl*a* were collected on each visit from three stations per lake, including the main station. Integrated samples from the trophogenic zone were collected from the three stations with weighted Tygon tubing and pooled into one sample. Water samples were stored in Nalgene bottles as described in Prepas and Trew (1983) and were refrigerated prior to analysis. From March to September 1984, discrete samples for determination of dissolved oxygen concentration (DO) were collected from the water column at the three stations with a 1.5-L aluminum drop-sleeve water bottle, at 0.5-m intervals from the lake surface to within 0.7 m of the lake bottom. The samples were stored in 50-mL glass-stoppered bottles and analyzed within 2 h. Samples for determination of phytobenthos Chl*a* were collected monthly from April to September 1984: a 500-mL polyethylene collection bottle, squeezed to expel air and provide suction, was connected to a polyethlyene tube that was moved over the surface of the lake sediments to suck up the top 2 to 3 cm of sediment and attached algae (Eaton and Moss 1966). Four to five samples were collected from each of two strata - a shallow stratum < 0.5 m depth and a deep stratum > 0.5 m depth, and the material pooled to make one sample per stratum. Shallow sediments were collected directly from marked areas while deeper sediments were collected with a 4-barrel corer (Hamilton et al. 1970) and the top 2 to 3 cm of each core sampled. All collected material

(sediment, phytobenthos, plus some lake water) was stored in 50-mL glass jars and refrigerated prior to analysis.

To estimate bacteria and zooplankton densities in the trophogenic zone, water samples were collected from 1 m below the surface of each lake. This depth was chosen as being representative of the trophogenic zone. As well, bacterial densities could be more easily compared with literature values since 1 m is the most common sampling depth for bacteria studies (Bird and Kalff 1984). Bacteria were collected monthly from April to August 1984 at the main station with a 1.5-L water bottle, zooplankton were collected biweekly during the ice-free season at three stations with a 40-L Schindler-Patalas trap (Schindler 1969) fitted with an 80-μm Nitex net. For bacteria counts, 15 mL of water was placed in 20-mL polyethylene vials and preserved with 5 mL of 40% phosphate buffered formalin pre-filtered through a 0.45-μm Millipore membrane filter. Zooplankton were either stored in 75-mL Nalgene bottles for dry weight determination or preserved with chilled 2% formalin with 6% sucrose (Prepas 1978) in 10-mL glass vials for species identification and enumeration. Zooplankton gut contents were determined on one sampling date; ten macrozooplankton of each species were anaesthetized with carbonated water prior to preservation (Haney and Hall 1973).

In 1984, primary production was determined biweekly at the main station in each lake. Water samples were collected from the appropriate depths, filtered through an 80-μm Nitex net to remove large zooplankton, and placed in 100-mL glass-stoppered light and dark bottles. Sets of two light and two dark bottles were suspended at 0.5-m intervals from 0.2 m below the lake surface to within 0.5 m of the lake bottom. Primary productivity was measured either as carbon uptake with inocula of 0.5 to 1.0 mL $NaH^{14}CO_3$ (1.5 MBq·mL^{-1}) per bottle or as oxygen evolution. Incubations took place between 0830 to 1400 and lasted 3 or 4 h. Immediately after incubation the bottles were stored in a light-tight container for 1 h prior to laboratory analysis.

Laboratory analysis

Within 48 h of collection, integrated water samples were analyzed for turbidity (Hach Model 2100a Turbidimeter), alkalinity (mg-L^{-1} $CaCO_3$; potentiometric method of Environment Canada), pH (Fisher Accumet digital pH metre), and specific conductivity (at 20 °C; YSI Model 31 Conductivity Bridge). Storage containers and glassware for chemical analyses were cleaned as in Bierhuizen and Prepas (1985). Glassware used in experiments with radioisotopes was soaked for 24 h in 2% Decon-75 (BDH Chemicals) and then cleaned as other glassware.

Water samples for phosphorus determination were analyzed as total phosphorus (TP; filtered through a 243-*u*m mesh Nitex net) and total dissolved phosphorus (TDP; filtered through a pre-rinsed 0.45-*u*m HAWP Millipore membrane filter) by the potassium persulfate method of Menzel and Corwin (1965) modified by Prepas and Rigler (1982), and as soluble reactive phosphorus (SRP; filtered as for TDP) by the molybdenum blue method of Murphy and Riley (1962). All samples were filtered within 6 h of collection; TP and TDP determinations were made within 48 h, SRP determinations within 24 h. To determine whether a significant amount of particulate phosphorus could pass through the 0.45 *u*m filter size, replicate water samples were filtered through the 0.45-*u*m filters and 0.20-*u*m Nuclepore polycarbonate filters monthly from June to August 1984. Differences in dissolved phosphorus concentrations between TDP estimates averaged 0.5% with a maximum of 3.4%. The estimates were statistically indistinguishable for all lakes: probabilities for each lake were calculated for the difference between TDP estimates with the two filter sizes for each date (two-way ANOVA) then, since sample size was so small the probabilities were combined for all lakes with $X^2 = 3.24$, $df = 6$, $P > 0.75$ (Sokal and Rohlf 1981: Box 18.1). TDP $<$ 0.45 *u*m (henceforth simply TDP) thus accurately represents dissolved phosphorus in the lakes. While TP levels in the saline lakes reached 16,000 *u*g-L^{-1}, the analytical technique used for determination of phosphorus was non-linear for TP levels $>$ 500 *u*g-L^{-1}. Consequently, water samples from the saline lakes were diluted with double distilled water (DDW) in a ratio of 1:10 for Fluevog and Peninsula Lakes and 1:50 for Oliva Lake. Samples for nitrogen determination were analyzed as total Kjeldahl nitrogen (TKN) and ammonia with the phenolhypochlorite method of Solorzano

(1969) and as nitrate-nitrite (NO_2-NO_3) with the cadmium-copper reduction method of Stainton et al. (1977), with techniques described in Prepas and Trew (1983). To be within the working range of the analytical techniques employed, water samples for TKN determination were diluted with DDW in ratios of 1:3 for Fluevog and Peninsula Lake and 1:5 for Oliva Lake. Total nitrogen (TN) was calculated as the sum of TKN and NO_2-NO_3.

For phytoplankton Chl*a* determination, water samples were filtered through Whatman GF/C filters, frozen and analyzed within 2 wk of collection by the ethanol extraction technique of Ostroksky outlined in Bergmann and Peters (1980) with no corrections for phaeophytins. For phytoplankton species identification, 75 mL of the original sample were preserved with Lugol's solution, then observed under a Wild M40 inverted microscope. Within 48 h of collection, the phytobenthos samples (pooled per stratum) were thoroughly mixed in the collection jars to produce a slurry and the volume recorded. A subsample was placed in a 20-mL culture tube with 10 mL ethanol for 24 h ethanol extraction. Samples were then placed in 50-mL plastic centrifuge tubes and spun for 10 min at 3200 rpm and 1500xg Relative Centrifugal Force in an International Clinical Centrifuge Model CL to separate the sediment and algal chlorophyll. The overlying water, dislodged algae and chlorophyll were placed in 20-mL culture tubes and Chl*a* was measured as outlined for phytoplankton. To compare the relative importance of phytobenthos to phytoplankton, phytobenthos Chl*a* was first converted to an areal estimate ($mg \cdot m^{-2}$, stratum weighted) then to a volumetric equivalent ($\mu g \cdot L^{-1}$) assuming the phytobenthos ($\mu g \cdot stratum^{-1}$) was mixed into the water overlying each stratum.

Samples for bacterial analysis were diluted with DDW in a ratio of 1:5 and filtered onto 0.20-μm Nuclepore polycarbonate filters. Samples were then enumerated within 2 wk of collection by D. Bird (McGill Univ.) with the epifluorescent DAPI stain method (Coleman 1980). To determine zooplankton dry weight, the sample volume was recorded and subsamples were filtered onto pre-weighed and pre-dried Whatman GF/C filters within 12 h of collection. The filters were frozen for up to 2 wk, then oven-dried at 60 °C for 24 h, cooled in a desiccator, and weighed on a Cahn Model G-2 Electrobalance (similar to Gurtz et al. 1980) with a

measured error of ± 0.09 mg. Zooplankton species were identified and enumerated in a modified plexiglas Bogorov counting chamber (Gannon 1971) with a Wild M3 dissecting microscope. For abundant species, subsamples containing a minimum of 100 individuals were counted while for rarer species the entire sample was counted.

Analysis of DO by the Winkler technique (Carpenter 1965) and analysis of ^{14}C primary productivity by the acid-bubbling technique (Schindler et al. 1972) were not suitable for this study since the addition of acid to the saline water caused effervescence and loss of sample. DO was determined with the Miller method for inland saline waters (Walker et al. 1970). For Fluevog and Peninsula Lake, ^{14}C primary productivity was satisfactorily analyzed after filtration and acid-fuming (Lean and Burnison 1979); the relationship between filtered volume and DPM (isotope disintegrations per minute as measured on the scintillation counter) was linear as long as a maximum 30 mL of inoculated sample was filtered. After filtration, the filters were fumed for 2 h in glass scintillation vials then 5 mL of Bray's scintillation fluor (Bray 1960) was added and the samples were counted on a Tracor Analytic Mark III 6881 Liquid Scintillation Counter with an automatic quenching correction. For Oliva Lake, primary productivity was estimated by changes in DO; these changes were converted to carbon uptake with a Photosynthetic Quotient (PQ) of 1.2 (Cole 1983). With both the ^{14}C and oxygen methods, primary productivity was calculated as light minus dark bottle readings. In Oliva Lake, ^{14}C primary productivity could not be determined since biological uptake of carbon was obscured by high chemical uptake (> 1500 mg $C \cdot m^{-3} \cdot h^{-1}$). Carbon uptake rates in Oliva Lake water "killed" with concentrated formalin were statistically indistinguishable from uptake rates in water that received no formalin (paired t-test: $t_{11} = 1.78$, $P > 0.10$). In Fluevog and Peninsula Lakes, water samples killed with formalin had low chemical uptake rates of carbon (< 20 mg $C \cdot m^{-3} \cdot h^{-1}$).

Orthophosphate uptake rates were determined in each lake with carrier-free $^{32}P\text{-}PO_4$ (New England Nuclear) five times over the periods from June to August 1983 and April to August 1984. For these assays, replicate experiments in which 1 mL of $^{32}P\text{-}PO_4$ (74 $KBq \cdot mL^{-1}$)

was added to 300 mL of lake water, were run for 3 - 6 h at lakeside and for up to 4 d in the laboratory. The assay method of Lean and Rigler (1974) was slightly modified; Millipore Swinnex 25-mm disc filter holders fitted with 0.45-*um* HAWP Millipore membrane filters were used for filtration. Filters with labelled lake water were placed in polyethylene scintillation vials, 5 mL of Bray's Fluor was added, and the samples counted within 48 h on the scintillation counter. The ^{32}P-PO_4 tracer batch was assessed in uptake experiments with water from two freshwater lakes in Alberta; orthophosphate turnover rates were rapid (as previously reported by Prepas 1983) indicating that the tracer was available for algal uptake. Laboratory bioassays to determine factors limiting algal growth in the study lakes were run with water collected from the trophogenic zone; all experiments were repeated twice with 3 - 4 replicates per treatment (experiment + control). Lake water filtered through 0.45-*um* filters, together with an unfiltered inoculum of native algae plus the bioassay treatment, was placed in 250-mL Erlenmeyer flasks beside a window that received full sunlight. Samples were shaken twice daily to prevent algal sedimentation and incubated for 2 wk prior to Chl*a* analysis. Phosphorus, inorganic nitrogen, general nutrient and iron limitation were tested by additions of KH_2PO_4 in phosphorus levels double the TP concentrations in the lake controls, either KNO_3 or NH_4Cl in nitrogen levels 1.5, 2 and 4 times the TN concentrations in the controls, soil extract solution (SE; prepared by autoclaving garden soil in DDW; Carmichael and Gorham 1974) in levels of 20 mL SE per L of lake water, and iron chelate EDTA in levels of 0.2 and 0.4 mM per flask, respectively. EDTA has been used to increase ferric iron solubility and bio-availability in previous limnological studies (e.g. Shubert 1978, Murphy et al. 1983).

Zooplankton grazing experiments were performed twice from June to August 1984 in Fluevog and Oliva Lakes. For these experiments, water was collected from 0.2 m below the lake surface and filtered through an 80-*um* Nitex net into 100-mL glass-stoppered bottles. In the two experimental bottles, large grazers (cladocerans and copepods in Fluevog Lake and *Artemia* in Oliva Lake) were added in densities equal to those in the lake the previous week (see Appendix E, Table E10), while no zooplankton were added to the two control bottles. The

bottles were suspended at 0.2 m below the lake surface for 2 h. The short incubation time was consistent with other grazing studies (4 h: Gulati 1975; 2 to 4 h: Hargis 1977). For this study, calculations indicated that if each 25 *u*g dry weight of zooplankton required 0.02 mg C·d^{-1} for maintenance and growth (after Lampert 1977; see Results) then the 2 h incubation would be sufficient to see a measurable effect of grazing on algal Chl*a* levels in the bottles with the zooplankton densities used, of at least 50% of the control Chl*a* levels in Fluevog Lake and up to 100% in Oliva Lake. The short incubation time would minimize the build up of bacteria populations as well. After incubation, samples were preserved with 1 mL of concentrated formalin and analyzed for Chl*a*. Addition of formalin did not interfere with Chl*a* analysis; in a laboratory test, Chl*a* readings were similar for samples with and without formalin (unpaired t-test: $t_{14} = 0.48$, $P = 0.64$).

Data manipulations

Mean growing season (May to September) phosphorus, nitrogen, and phytoplankton Chl*a* levels were calculated as averages of the integrated samples collected from the trophogenic zone. Mean growing season rates of primary productivity (V) were calculated from daily values which were volume weighted over the trophogenic zone. Whole lake conductivity estimates were calculated from data from discrete samples, volume weighted over the water column. Measured mean growing season Chl*a* and V values were compared to values predicted by the empirical models of Smith (1982) and Smith (1979), the former model based on TP, TN and Chl*a* data from 127 freshwater lakes, and the latter based on TP, Chl*a* and V data from 49 freshwater lakes. Measured summer densities of bacteria were compared to those predicted by Bird and Kalff's (1984) model based on bacteria and Chl*a* data from 39 freshwater, marine and estaurine systems. Measured mean growing season zooplankton biomass was compared to that predicted by McCauley and Kalff's (1981) model based on zooplankton and phytoplankton biomass data from 17 freshwater lakes. Zooplankton dry weight and Chl*a* were converted to wet weight and phytoplankton biomass, respectively, as suggested by McCauley and Kalff

(1981). 95% and 50% confidence limits for points outside the regression data sets were calculated about predicted Chl*a* and V values with data from Smith (1979) and V.H. Smith (Univ. of North Carolina *unpubl.*); in some cases 95% confidence limits were too wide to be meaningful since predicted values were far outside the original data set. Similar 95% confidence limits were calculated about predicted bacteria densities with information from Bird and Kalff (1984), and about McCauley and Kalff's (1981) phytoplankton - zooplankton relationship from Prepas (1984). The empirical models described are listed in Appendix D.

Statistical analyses followed Snedecor and Cochran (1980) and Sokal and Rohlf (1981) and were performed with BMDP statistical software on the Amdahl computer 580/5860 at the University of Alberta. Data collected in 1983 were similar to those collected in 1984 unless otherwise stated.

C. Results

Description of the study lakes

The three saline lakes - Fluevog, Peninsula and Oliva - are located in aspen prairie-parkland 150 km east of Edmonton, Alberta (Fig. 2.1) and are surrounded by a mixture of ranch land and cultivated fields (primarily canola and flax). Annual rainfall in the region averages 300 mm while annual lake evapotranspiration averages 600 mm (Fisheries and Environment 1978). Average summer wind speeds are 13 km-h^{-1} (Environment Canada 1984). All of the lakes were shallow (mean depths 1.3 - 2.1 m) with small surface areas ($<$ 140 ha - Table 2.1) and simple bowl-shaped basins. There were no permanent surface inflows or outflows from the lakes (see Appendix B for morphometric maps of the lakes). Drainage basin areas were 307, 1870 and 376 ha in Fluevog, Peninsula and Oliva Lakes, respectively. Average summer turbidity was less than 15 JTU in Fluevog and Peninsula Lakes and less than 2 JTU in Oliva Lake. The average summer Secchi Disc (SD) readings in both Fluevog and Peninsula Lakes were between 0.6 and 0.8 m. while in Oliva Lake, the SD was always visible on the lake

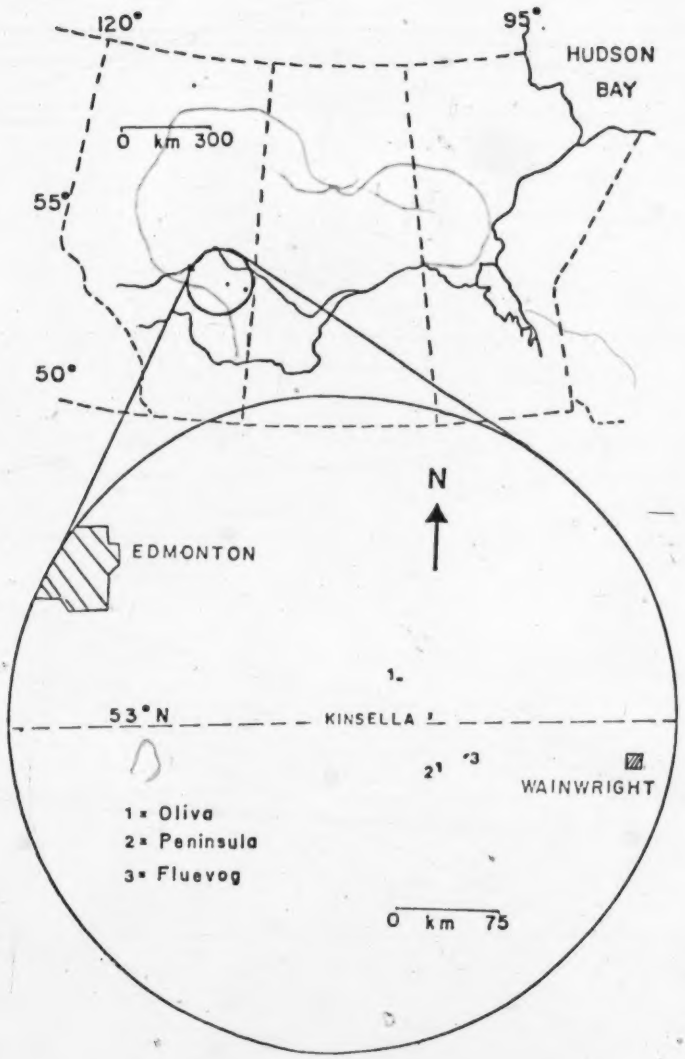

Figure 2.1: The location of the three saline study lakes in Alberta.

Table 2.1: The location and morphometry of the three saline study lakes.

Lake	Lat.- (°N)	Long.- (°W)	Max. Depth (m)	Mean Depth (m)	Surface Area (ha)
Fluevog	52° 50'	111° 19'	2.1	1.4	32
Peninsula	52° 52'	111° 29'	3.1	2.1	138
Oliva	53° 05'	111° 36'	1.7	1.3	52

bottom at 1.6 to 1.7 m. The three lakes are thus distinct from the highly turbid (*argillotrophic*) saline system in central Alberta studied by Daborn (1975).

Average summer conductivities ranged from 9,400 and 13,400 umhos-cm^{-1} in Fluevog and Peninsula Lakes, respectively, where Na^+ and SO_4^{2-} were the dominant ions, to 55,000 umhos-cm^{-1} in Oliva Lake where Na^+, SO_4^{2-} and CO_3^{3-} were the dominant ions. (Details of ionic composition and TDS levels are in Bierhuizen and Prepas 1985: TDS in Oliva Lake was overestimated due to water retention and crystallization in the highly saline samples; American Public Health Association 1981). Mean summer iron concentrations were 2.1, 1.5, and 0.6 mg-L^{-1} in Fluevog, Peninsula and Oliva Lakes, respectively (Bierhuizen and Prepas 1985). Both Fluevog and Peninsula Lakes were isothermal over the year (Figs. 2.2, 2.3 and 2.4). Only Oliva Lake exhibited inverse summer stratification based on vertical profiles of conductivity and temperature (Figs 2.4, 2.5 and Appendix A). The lakes were never anoxic from March to September 1984, DO levels were always $>$ 3 mg-L^{-1} (Fig. 2.6). Average summer pH was 9.2, 9.2 and 9.9, and alkalinity ($CaCO_3$ mg-L^{-1}) was 2160, 2600 and 22,660 in Fluevog, Peninsula and Oliva Lake, respectively. Thus, all three lakes can be characterized as alkaline, saline systems.

Species of plants and animals found in the study lakes were similar to those reported for other saline lakes in western Canada (Hammer et al. 1975; Hammer et al. 1983; R.S. Anderson, Alberta Environment, pers. comm.) and species diversity was low as is typical of highly saline environments (Williams 1972). The dominant phytoplankton species were *Microcystis aeroginosa* in Fluevog Lake, *M. aeroginosa* and *Lyngbya Birgei* in Peninsula Lake, and a *Cryptomonas* sp. plus small ($<$ 30 um long) diatoms such as *Fragilaria* and *Navicula* in Oliva Lake. Unidentifiable debris in the settling chambers made phytoplankton identification difficult. The major phytobenthos species were *Rhizoclonium hieroglyphicum* in Fluevog and Peninsula Lakes, and an unidentified filamentous green alga (*Pithophora* sp.?) in Oliva Lake. Macrophytes were scarce with only some *Ruppia* and *Carex* sp. present. There were only three species of zooplankton in each lake: *Diaptomus nevadensis*, *Diaptomus sicilis* and *Daphnia*

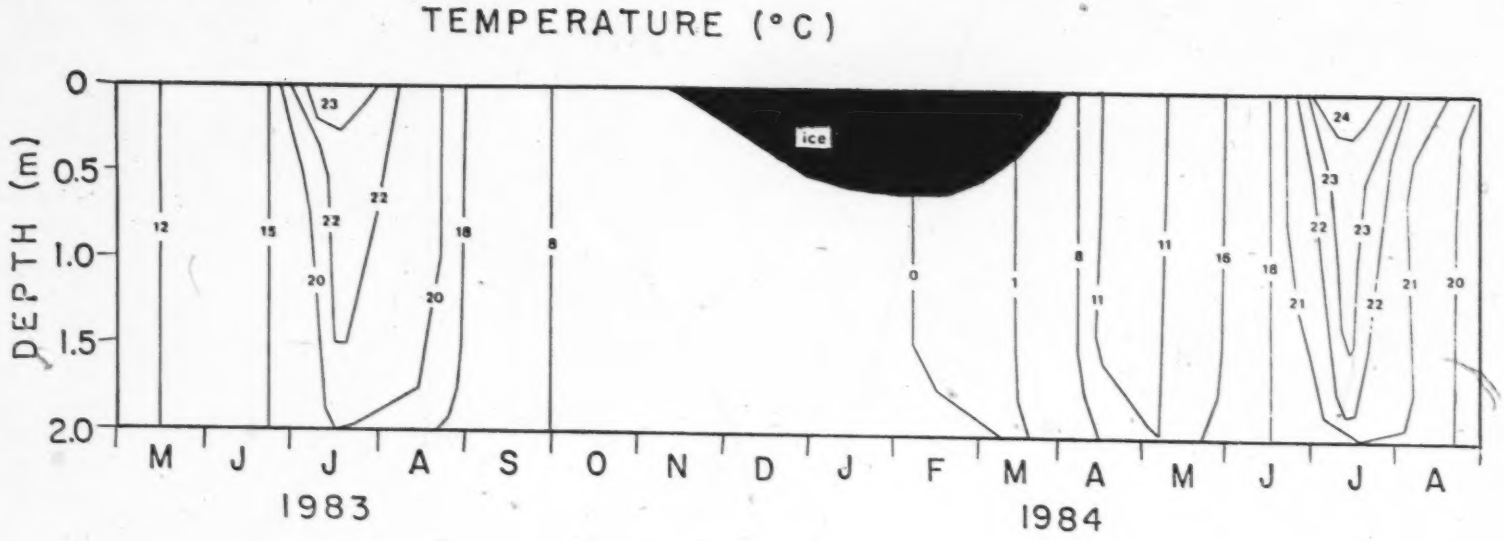

Figure 2.2: Depth-time diagram of isotherms (°C) for Fluevog Lake from May 1983 to September 1984.

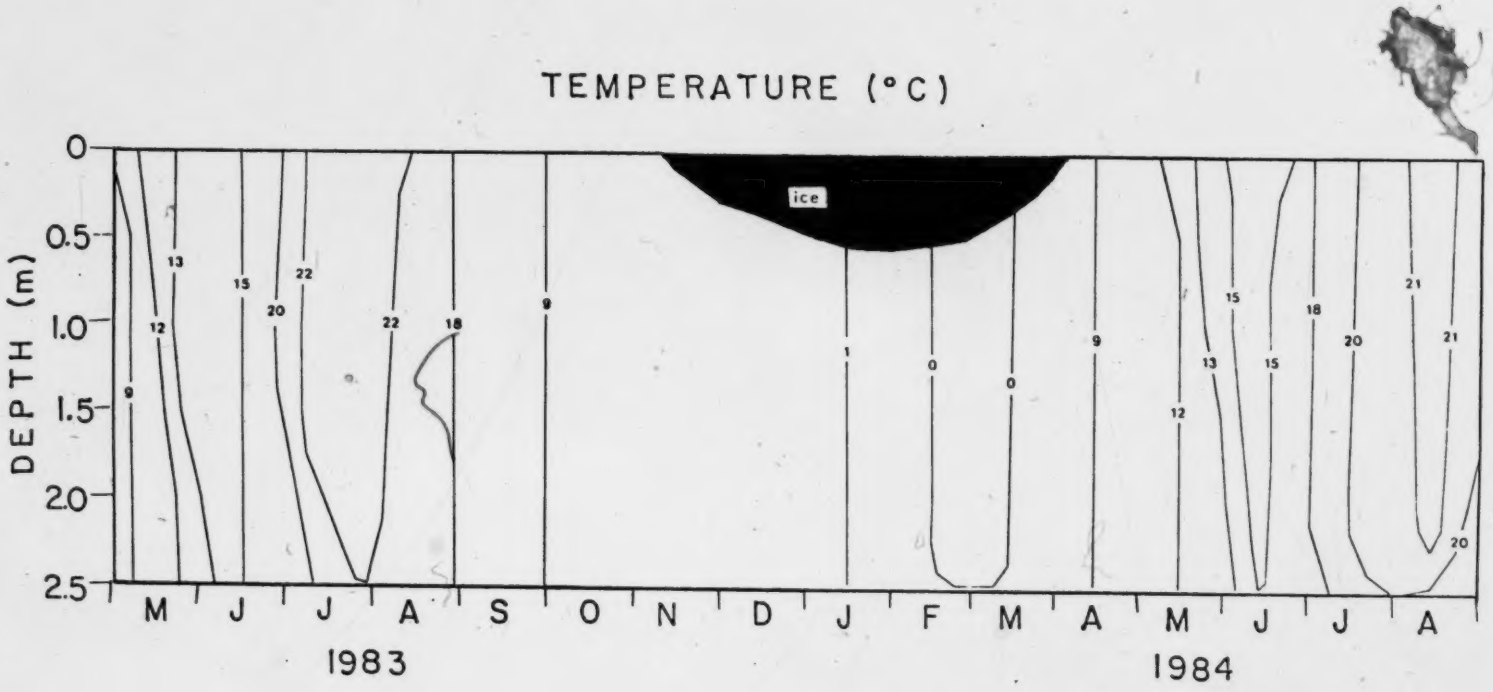

Figure 2.3: Depth-time diagram of isotherms (°C) for Peninsula Lake from May 1983 to September 1984.

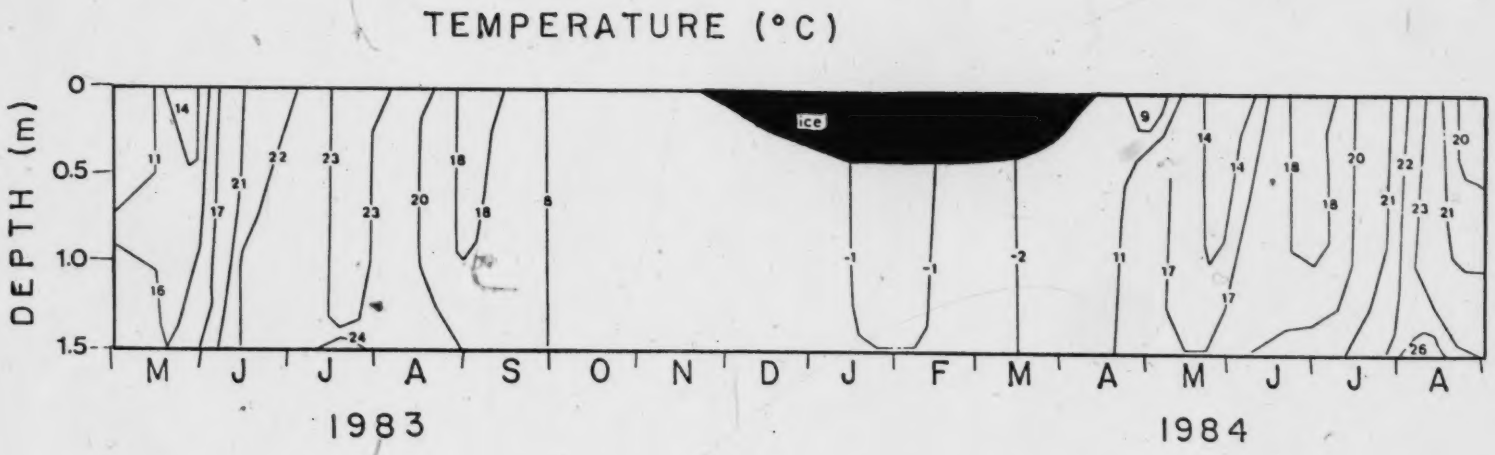

Figure 2.4: Depth-time diagram of isotherms (°C) for Oliva Lake from May 1983 to September 1984.

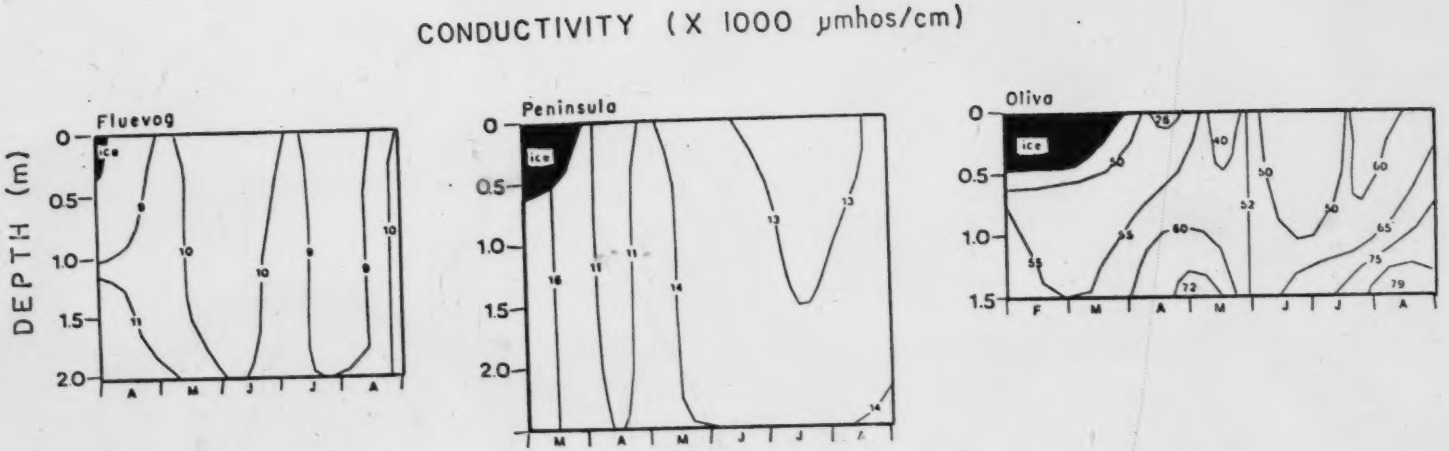

Figure 2.5: Depth-time diagram of isopleths of specific conductivity (umhos-cm^{-1}) for the three saline lakes from February, March or April to September 1984.

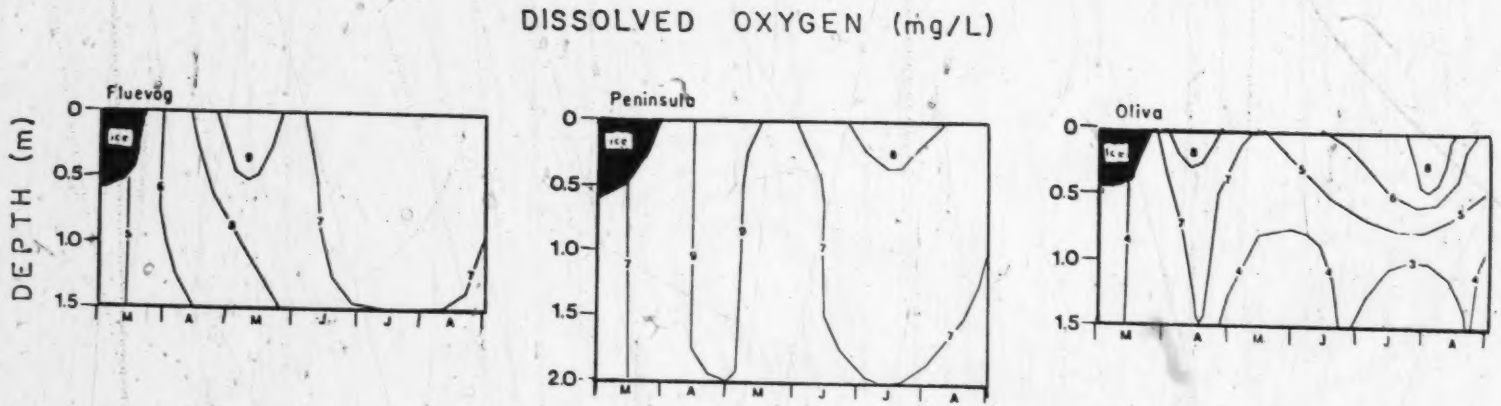

Figure 2.6: Depth-time diagram of isopleths of dissolved oxygen ($mg \cdot L^{-1}$) for the three saline lakes from March to September 1984.

similis in Fluevog and Peninsula Lakes, and *Artemia salina*, *Brachionus plicatilis* and a *Hexarthra* sp. in Oliva Lake. *Ephydridae* larvae were abundant during the summer in Oliva Lake. *Hyallela azteca* were common in Fluevog and Peninsula Lakes. The lakes were fishless.

Chla, primary productivity and nutrient levels

Mean growing season TP, TDP and TN levels were extremely high in all three study lakes: TP and TN varied from 2,300 to over 11,500 $ug\text{-}L^{-1}$, and TDP from 94 to 96% of TP. TN:TP ratios (by weight) were low, ranging from 0.9 to 1.7 (Table 2.2). Despite the extremely high TP and TN levels, mean growing season phytoplankton Chl*a* levels were extraordinarily low in all the lakes ($\leq$ 10 $ug\text{-}L^{-1}$; Table 2.3). Phytobenthos Chl*a* levels were also low (mean areal estimates $\leq$ 72 $mg\text{-}m^{-2}$ and mean volumetric equivalents $\leq$ 50 $ug\text{-}L^{-1}$; Table 2.3). In Oliva Lake, phytobenthos was considerably more abundant than phytoplankton (50 compared to 4 $ug\text{-}L^{-1}$), whereas in the other two study lakes, the two algal communities were of similar size. However, even the combination of phytoplankton and phytobenthos Chl*a* levels (17, 18, and 54 $ug\text{-}L^{-1}$ for Fluevog, Peninsula and Oliva Lakes, respectively) were very low relative to TP and TN levels. The measured Chl*a* levels were compared to predicted levels based on TP and TN levels and Smith's (1982) empirical model. The measured phytoplankton Chl*a* levels were $<$ 2% of the predicted levels and the combined phytobenthos and phytoplankton Chl*a* levels were $<$ 5% of the predicted values (Table 2.3), well outside the 50% confidence limits for the predicted values. Therefore, the combined phytoplankton and phytobenthos communities were not large enough to be a major nutrient sink.

Measured mean growing season rates of primary productivity (V) in each lake varied from 17 to 156 $mg\ C\text{-}m^{-3}\text{-}d^{-1}$ (Table 2.4). Measured V values were similar to predicted values based on measured phytoplankton Chl*a* and Smith's (1979) empirical model. In contrast, the measured V values were 3 to 4 orders of magnitude less than predicted values based on TP levels and Smith's (1979) model, and fell outside the 95% confidence limits for the predicted rates (Table 2.4). Mean phytoplankton primary productivity:Chl*a* ratios for the growing

Table 2.2: 1984 mean growing season total phosphorus (TP), total dissolved phosphorus (TDP) and total nitrogen (TN) levels in the trophogenic zone of the study lakes.

Lake	TP ($ug\text{-}L^{-1}$)	TDP ($ug\text{-}L^{-1}$)	TN ($ug\text{-}L^{-1}$)	TN:TP
Fluevog	2,310	2,165	3,923	1.7
Peninsula	3,658	3,502	4,178	1.1
Oliva	13,304	12,817	11,517	0.9

Table 2.3: Comparison of 1984 measured mean growing season phytoplankton and phytobenthos chlorophyll (Chl*a*) in the study lakes with predicted phytoplankton Chl*a* based on measured total phosphorus (TP) and total nitrogen (TN) and Smith's (1982) empirical model.

Lake	Phytoplankton Chl*a* ($\mu g \cdot L^{-1}$)	Phytobenthos Chl*a* ($mg \cdot m^{-2}$)	Phytobenthos Chl*a* ($\mu g \cdot L^{-1}$)	Predicted Chl*a* ($\mu g \cdot L^{-1}$)	50% Confidence Limits
Fluevog	3	19	14	450	80 - 2,600
Peninsula	10	17	8	700	90 - 4,980
Oliva	4	72	50	2,500	180 - 35,360

Table 2.4: Comparison of 1984 measured mean growing season primary productivity (V) in the trophogenic zone of the study lakes with productivity predicted from measured phytoplankton chlorophyll (Chl*a*) or total phosphorus (TP) and Smith's (1979) empirical models.

Lake	V Observed ($mgC\text{-}m^{-3}\text{-}d^{-1}$)	V Predicted from Chl*a* ($mgC\text{-}m^{-3}\text{-}d^{-1}$)	50% Confidence Limits	V Predicted from TP ($mgC\text{-}m^{-3}\text{-}d^{-1}$)	95% Confidence Limits
Fluevog	32	31	0 - 132	23,950	22,100 - 25,790
Peninsula	156	176	80 - 270	37,960	35,040 - 40,890
Oliva	17	48	0 - 149	138,280	127,590 - 148,970

season were 11, 16 and 4 for Fluevog, Peninsula and Oliva Lakes, respectively, and were comparable to productivity:Chl*a* ratios for other saline and freshwater lakes (Hammer 1981; Wetzel 1983). Therefore phytoplankton were not turning over unusually fast in the study lakes.

^{32}P-PO_4 uptake was not detectable in any of the study lakes; orthophophate turnover times approached $+\infty$ (Lean and Rigler 1974) and thus biologically available phosphorus was abundant in the lakes. In all the lakes, > 80% of summer TP was SRP. In contrast, in freshwater lakes (TDS < 500 mg-L^{-1}) in central Alberta which cover a spectrum of depths and productivity levels, 1 to 42% of summer TP was SRP (Prepas 1983). In bioassays with the saline lake waters (see Appendix E, Table E8), the additions of KH_2PO_4 did not increase Chl*a* levels over control levels (split plot ANOVA to test treatment effects, with lakes and treatments as groups and experiment dates as subplots: $F_{1,12} = 0.36$, $P = 0.27$). Additions of KNO_3 in nitrogen concentrations 1.5, 2 and 4 times TN concentrations in the lakes increased Chl*a* levels by an average of 12, 7 and 18 times, respectively, over control levels in all lakes. Additions of NH_4Cl in nitrogen concentrations 1.5, 2 and 4 times TN concentrations in the lakes increased Chl*a* levels by an average of 5, 7 and 10 times, respectively, over control levels. In one experiment with Fluevog Lake water, additions of NH_4Cl at the '4 times' level caused no significant change in Chl*a* levels from control levels (*a posteriori* Dunnett's test with total MS*error* from split-plot ANOVA: $P > 0.05$). In the 17 other cases, addition of inorganic nitrogen significantly increased Chl*a* over control levels (Dunnett's test: $P < 0.05$ for all lakes, treatments and dates). Variability in Chl*a* levels among flasks was greatest with the highest additions of inorganic nitrogen (i.e. the '4 times' addition level). Additions of soil extract (SE) caused no increase in Chl*a* in any of the experiments (split plot ANOVA: $F_{1,12} = 0.53$, $P = 0.48$). Additions of EDTA caused no increases in Chl*a* levels in either Fluevog or Peninsula Lake water (Dunnett's test with total MS*error* from split-plot ANOVA: $P > 0.05$), but both the 0.2 and 0.4 mM additions of EDTA significantly increased Chl*a* levels in Oliva Lake water (Dunnett's test: $P < 0.05$) by an average of 1.4 and 2 times, respectively, over control levels. Thus, only inorganic nitrogen was consistently limiting to algal growth in all the lakes, while

there was evidence of iron limitation in Oliva Lake. Phytoplankton species present in all bioassay experiments, mainly *Microcystis aeroginosa* in Fluevog and Peninsula Lake water and various small diatoms in Oliva Lake water, were species found naturally in the lakes.

Bacteria and zooplankton

Pelagic bacterial densities in the study lakes ranged from 1.2 X 10^7 to 2.3 X 10^7 cells-mL^{-1}. These densities are 2 to 8 times higher than predicted densities based on phytoplankton Chl*a* levels and Bird and Kalff's (1984) empirical model (Table 2.5) and outside the 95% confidence limits about the predicted values, except in Peninsula Lake. Most bacteria in the study lakes were smaller than bacteria in freshwater lakes (0.40 *u*m diameter as compared with 0.60 *u*m; D. Bird, McGill Univ. *pers. comm.*). Total bacteria numbers in the lakes were probably underestimated since bacteria in the lake sediments were not sampled. Zooplankton were also abundant in the lakes; mean growing season zooplankton dry weights were 1.3, 1.4, and 8.2 mg-L^{-1} in Fluevog, Peninsula and Oliva Lakes, respectively. Zooplankton wet weight in each lake was an order of magnitude higher than that predicted from measured phytoplankton biomass and McCauley and Kalff's (1981) empirical model (Fig. 2.7). Hence, both bacteria and zooplankton populations were larger than expected from the size of the phytoplankton standing crop.

To evaluate whether algal and bacterial populations in the lakes were sufficient to support the zooplankton populations, daily carbon requirements of zooplankton were compared to carbon mass in the algae and bacteria. For minimum population growth, zooplankton populations in the lakes require 1.1, 1.2 and 6.5 mg-L^{-1} of carbon daily in Fluevog, Peninsula and Oliva Lakes, respectively. These calculations assume that each 25 *u*g dry weight of zooplankton requires 0.02 mg C-d^{-1} after Lampert (1977) who worked with 25 *u*g (dry weight) *Daphnia pulex*, and that data based on *D. pulex* can be applied to the total zooplankton community. Combined phytoplankton and phytobenthos carbon levels in the study lakes (carbon mass = 10 x Chl*a*; Frost 1972) were estimated at 0.17, 0.18 and 0.54 mg C-L^{-1},

Table 2.5: Comparison of 1984 measured mean summer bacterial densities at 1 m below the lake surface in the study lakes with densities predicted from mean summer phytoplankton chlorophyll (Chl*a*) and Bird and Kalff's (1984) empirical model.

Lake	Observed Bacteria (10^6 cells-mL^{-1})	Predicted Bacteria (10^6 cells-mL^{-1})	95% Confidence Limits
Fluevog	12	2	0.8 - 5.0
Peninsula	13	6	4.0 - 15.0
Oliva	23	3	2.0 - 4.0

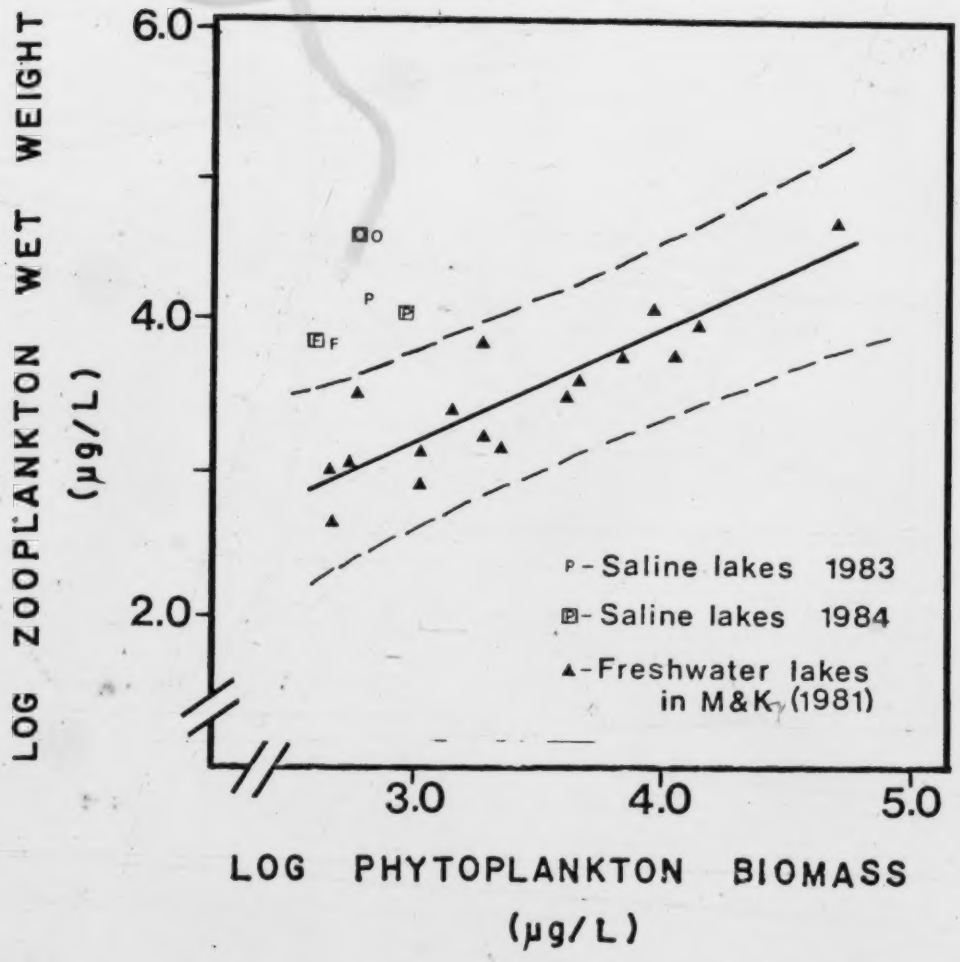

Figure 2.7: 1983 and 1984 log mean growing season zooplankton wet weight ($\mu g \cdot L^{-1}$) at 1 m below the lake surface related to log phytoplankton biomass ($\mu g \cdot L^{-1}$) in the trophogenic zone in the three saline lakes (F = Fluevog, P = Peninsula, O = Oliva) and data from 17 temperate freshwater lakes analyzed by McCauley and Kalff (M&K)(1981). Solid line represents McCauley and Kalff's model, dotted lines are 95% confidence limits about predicted values outside the model.

whereas carbon levels of bacteria populations (400 mg C per cell; Overbeck 1980) were estimated at 0.48, 0.52 and 0.92 $ug\text{-}L^{-1}$ in Fluevog, Peninsula and Oliva Lakes, respectively. Thus, algal populations in the saline lakes could supply only 8 to 16% of the carbon requirements for the zooplankton populations, while combined algal and bacteria populations would supply 22 to 60% of carbon requirements. For freshwater lakes in Alberta that cover a wide range of productivities (Prepas and Trew 1983; A. Trimbee and E.E. Prepas, University of Alberta, *unpubl.*), calculations indicate that mean summer phytoplankton populations would supply 61 to 84% of daily zooplankton carbon requirements and combined mean summer phytoplankton and bacteria populations would supply 140 to 600% of carbon requirements. Phytoplankton, a major food source for zooplankton in freshwater lakes, is thus insufficient to support the large zooplankton populations in the saline study lakes. Therefore, bacteria and detritus are likely an important zooplankton food source in the study lakes. This conclusion is supported by observations of zooplankton gut contents: in Oliva Lake, *Artemia salina* were primarily feeding on brown material (bacteria and detritus) while in Fluevog and Peninsula Lakes, the *Daphnia similis* and *Diaptomus sicilis* were feeding equally on brown material and green algal cells. Size ranges of bacterial and algal cells in the study lakes were within the range of particle sizes consumed by *Artemia* (Reeve 1963), cladocerans (Holtby and Knoechel 1985) and copepods (Haney 1973).

Despite the relatively high densities of zooplankton in the saline lakes, results from field experiments indicated that zooplankton grazers do not have a substantial effect on phytoplankton population growth. Phytoplankton Chl*a* levels (Appendix E, Table E9) were statistically indistinguishable in bottles with and without grazers in both Fluevog and Oliva Lakes (split plot ANOVA to test treatment effects, with lakes and treatments as groups and experiment dates as subplots: $F_{1,4} = 2.52$, $P = 0.17$). However, seasonal variation in both zooplankton dry weight and phytoplankton Chl*a* (Fig. 2.8) offer evidence of zooplankton grazing pressure. In Oliva Lake, even with low winter light levels, phytoplankton Chl*a* levels increased to 3.5 $ug\text{-}L^{-1}$ under the ice as *Artemia* populations disappeared and grazing pressure

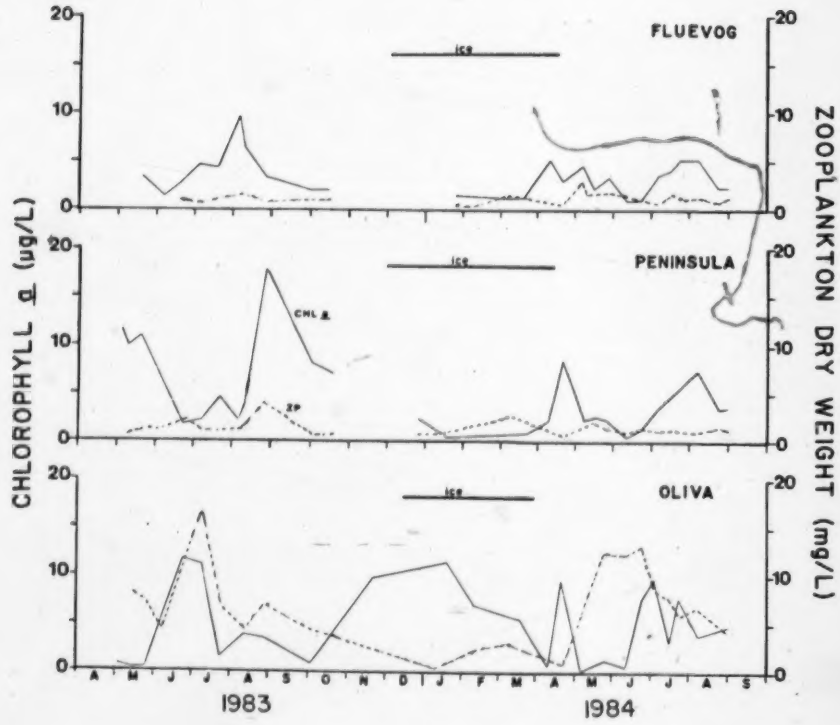

Figure 2.8: Seasonal variation in zooplankton dry weight (ZP, mg·L^{-1}) at 1 m below the lake surface and phytoplankton chlorophyll (Chl*a*,*u*g·L^{-1}) in the trophogenic zone for the three saline lakes from April 1983 to September 1984.

decreased, which suggests that the removal of grazing pressure allowed for increased algal growth. The increased Chl*a* levels, however, were still much lower than would be expected based on lake TP and TN levels. In Fluevog and Peninsula Lakes, similar winter decreases in zooplankton populations were not mirrored by increases in Chl*a* levels (Fig. 2.8), which suggests that grazing pressure had a relatively smaller effect on algal populations.

D. Discussion

It is clear from this study that the extraordinarily high concentrations of TP and TN in the study lakes are not effectively utilized by the algal communities. Phytoplankton and phytobenthos Chl*a* and phytoplankton primary productivity were all much lower than would be predicted from ambient nutrient levels and empirical models developed for freshwater lakes. Freshwater nutrient - productivity relationships thus do not appear to be valid for these prairie saline systems.

TP is definitely not limiting algal growth in the saline lakes, in contrast to many freshwater lakes. The negligible orthophosphate uptake rates and the high SRP levels (a good measure of orthophosphate in lakes with low orthophosphate turnover times; Peters and MacIntyre 1976) in the study lakes, combined with the lack of increased algal growth in bioassays spiked with KH_2PO_4, suggest that biologically available phosphorus is abundant and in quantitites well above short term algal requirements. TP may be acting as a conservative rather than a dynamic element in the study lakes; concentrations could then be related primarily to physical processes in the lakes. Seasonal changes in TP in the study lakes (see Appendix C) were associated with changes in lake volume: observed TP levels were not significantly different from levels calculated from a constant TP mass (determined for August 1983) corrected for changes in lake volume (paired t-test: $P > 0.20$ for all the lakes). As well, seasonal changes in TP levels and marker height above the lake surface (a measure of lake volume) were highly correlated (Fluevog $r = 0.92$, $n = 12$, $P = 0.001$; Peninsula $r = 0.64$, $n = 12$, $P = 0.02$;

Oliva $r = 0.77$, $n = 14$, $P = 0.001$). Aeolian loadings (14 mg TP·m^{-2} for the open water season; from Riley and Prepas 1983) supplied only a very small portion of the measured TP in the water column. These results support the idea that allochthonous input of TP was minimal and that TP levels were affected by physical rather than biological processes.

TN is also not limiting to algal growth in the study lakes, based on the extremely high Chl*a* levels predicted from measured TN and TP levels and Smith's (1982) model. However, TN in prairie saline lakes may not be a good indicator of biologically available nitrogen. Algal growth appeared to be limited by inorganic nitrogen: in the laboratory bioassays, Chl*a* levels were markedly increased when KNO_3 and NH_4Cl were added. However, addition of general nutrient SE solution failed to promote algal growth in any of the lake bioassays; nitrogen levels in the SE inoculum were relatively low (265 μg·L^{-1} TN). The levels of inorganic nitrogen needed to stimulate algal production in bioassay experiments suggest that nitrogen cycling may be different in the saline lakes as compared to fresh waters. In the saline lakes, inorganic nitrogen might be a useful indicator of biologically available nitrogen. The high pH levels in the study lakes may render much of the ammonia unavailable. At a pH above 9.0, as recorded in the three lakes, 30% of the measured ammonia levels would be present as toxic un-ionized ammonia (NH_3) (Trussell 1972). High toxic ammonia levels might explain decreased algal growth in some bioassays with Fluevog Lake water when high levels of NH_4Cl were added (i.e. the '4 times' addition level). Inorganic nitrogen limitation has been proposed in other saline lake studies, either from algal bioassays (Moss 1969; Stephens and Gillespie 1976) or from correlations between inorganic nitrogen levels and phytoplankton Chl*a* (Haertl 1976).

Iron limitation was detected only in Oliva Lake where additions of EDTA increased algal growth, a result similar to that observed in saline Devil's Lake, North Dakota (Shubert 1978). High pH levels in Oliva Lake (9.9) could reduce iron solubility (Stumm and Morgan 1981).

The high salinity of the three study lakes could influence algal productivity: some micronutrients might be less available or algal cells may suffer from extreme osmotic stress

(Por 1980). The ratio of specific ions could also influence productivity. The unproductive saline lakes in Alberta are dominated by the ions Na^+, SO_4^{2-} and CO_3^{3-} (Bierhuizen and Prepas 1985), as compared with freshwater lakes in Alberta that are dominated by Ca^{2+} and HCO_3^{2-} (Alberta Environment *unpubl.*). The ions Mg^{2+} and SO_4^{2-} are relatively more important in the saline lakes in western Canada (Topping and Scudder 1977; Barica 1978; Hammer 1978; Bierhuizen and Prepas 1985) than in saline lakes in other parts of the world (e.g. East Africa: Talling and Talling 1965, the western U.S.A.: Anderson 1958; Wetzel 1964; Armstrong et al. 1966, and Australia: Bayly and Williams 1966). Outside of western Canada, some saline lakes can be extremely productive with phytoplankton Chl*a* levels > 500 $ug\text{-}L^{-1}$ despite TDS > 5000 $mg\text{-}L^{-1}$ (Melack and Kilham 1974 in East Africa; Armstrong et al. 1966 and Walker 1975 in the western U.S.A.; Hammer 1981 in Australia). Phytobenthos (periphyton) Chl*a* levels > 300 $mg\text{-}m^{-2}$ have been reported for saline lakes in the western U.S.A. (Castenholz 1960; Wetzel 1964). Although the major difference between the unproductive saline lakes of western Canada and productive saline lakes elsewhere appears to be the relative importance of Mg^{2+} and SO_4^{2-}, the effects of specific ion ratios on algal growth need further investigation.

Some of the low algal productivity in the Alberta saline lakes may be explained by biological interactions with bacteria and zooplankton. In the study lakes, bacterial densities are high relative to the phytoplankton Chl*a* levels and to bacterial densities in freshwater lakes (Bird and Kalff 1984) although similar to densities reported for other saline lakes (Mason 1967; Kilham 1981). The bacteria in the study do not seem to be competing with algae for orthophosphate (low $^{32}P\text{-}PO_4$ uptake rates in the lakes incorporate both bacterial and algal uptake), but they may be competing with algae for other nutrients. Zooplankton biomass in the study lakes was also extremely high relative to phytoplankton Chl*a* levels. Seasonal variation in zooplankton dry weight and phytoplankton Chl*a* in the three saline lakes indicated possible grazer control of algal biomass, particularly in Oliva Lake, although the relationship is obscured by much random variation in seasonal zooplankton and phytoplankton biomass. Nonetheless, even in the absence of grazers (as in the laboratory bioassays), Chl*a* levels did not increase to

the extraordinary high levels that would be expected from the high levels of TP and TN in the lakes. Some other inhibitor of algal growth, possibly chemical, is thus implicated. The field experiments in this study did not indicate particularly heavy grazing pressure. However, zooplankton grazing pressure on bacteria, although not quantified, was probably high in the study lakes as a result of insufficient algal biomass available for zooplankton population growth and thus would lessen the measured grazing pressure on algae. In other saline lakes with zooplankton densities similar to those reported in this study, removal of grazers from containers reportedly increased algal growth although these observations were not supported by statistics (Anderson 1958; Mason 1967). However, these grazing experiments were allowed to run for an average of 124 h (Anderson 1958) and 120 d (Mason 1967) and thus are difficult to compare with the 2 h experiments in this study. Field observations from other studies also suggest that zooplankton in saline lakes, particularly *Artemia salina*, can decrease algal standing crop in small saline systems (Por 1980; Javor 1983). To accurately determine the role of grazers in prairie saline lakes, zooplankton grazing rates need to be studied in greater detail.

Thus, the cycling of organic material in saline lakes may differ from those observed in freshwater lakes. Algal biomass is a relatively small part of the total biomass of the saline lakes, in contrast to the freshwater lakes in this region, and is insufficient to maintain the existing zooplankton populations. Consequently, abundant bacteria and detritus are probably an important food source for zooplankton grazers in the saline lakes, (observed for *Artemia salina* in Solar Lake, Sinai; Cohen, reported in Por 1980), as is occassionally true for some oligotrophic freshwater lakes (Gulati 1975). Prairie saline lakes are therefore ideal locations for the study of role of bacteria and detritus in zooplankton feeding.

The low algal productivity of the saline study lakes is thus influenced by a combination of factors: possible inorganic nitrogen limitation, competition for nutrients with large bacterial populations, and high zooplankton grazing pressure. Physiological inhibitions due to high salinity levels and the relative concentrations of Mg^{2+} and SO_4^{2-} need to be examined.

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III. General Discussion

It is apparent from this study that prairie saline lakes are biologically and chemically unique ecosystems. Despite extraordinarily high levels of both total phosphorus and total nitrogen ($>$ 2,000 $ug\text{-}L^{-1}$), the three saline study lakes in eastern Alberta had very low phytoplankton chlorophyll *a* levels ($<$ 10 $ug\text{-}L^{-1}$). In each lake, combined levels of both phytoplankton and phytobenthos chlorophyll *a* were $<$ 5% of chlorophyll *a* levels predicted from total phosphorus and total nitrogen levels and Smith's (1982) model developed for freshwater lakes. Measured rates of phytoplankton primary productivity indicated that there was no unusually rapid turnover of phytoplankton populations in the lakes - productivity rates were similar to those predicted from measured phytoplankton chlorophyll *a* levels in the lakes and 3 to 4 orders of magnitude less than those predicted from measured total phosphorus levels, both predictions based on Smith's (1979) models for freshwater lakes. Evidently, neither the phytoplankton nor the phytobenthos communities were making use of the high total phosphorus and total nitrogen concentrations in the study lakes.

The disagreement between measured chlorophyll *a* levels and primary productivity rates with predicted values indicates that models developed for freshwater lakes are not appropriate for these saline systems. In the three study lakes, high levels of total phosphorus were probably representative of biologically available phosphorus, as levels of soluble reactive phosphorus were high, orthophosphate uptake rates were negligible, and KH_2PO_4 additions to laboratory bioassays did not stimulate algal growth. The high total nitrogen levels were not good indicators of biologically available nitrogen; total nitrogen did not appear to limit algal growth based on the empirical models developed for freshwater systems. Inorganic nitrogen, in contrast, did limit algal growth in laboratory bioassays. Consequently, total nitrogen and inorganic nitrogen appear unrelated in prairie saline lakes. Iron limitation was demonstrated for Oliva Lake only which suggests that iron was sufficiently abundant and biologically available for algal growth in Fluevog and Peninsula Lakes.

Productivity differences in saline lakes may be related to differences in ions in the lakes. The dominant ions in the study lakes (Mg^{2+}, SO_4^{2-}, CO_3^{3-}; Bierhuizen and Prepas 1985) differ from the dominant ions in most freshwater systems (Ca^{2+}, CO_3^{3-}/HCO_3^{2-}; Rodhe 1949). Mg^{2+} and SO_4^{2-} are also much more abundant in the unproductive saline lakes of western Canada (Barica 1978; Hammer 1978; Bierhuizen and Prepas 1985) compared to the productive saline lakes of East Africa (Talling and Talling 1965), the western U.S.A. (Anderson 1958; Wetzel 1964; Armstrong et al. 1966) and Australia (Bayly and Williams 1966). However, the exact effects of ionic ratios and specific ions such as Mg^{2+} and $S0_4^{2-}$ on lake productivity are not well understood.

Bacteria densities and zooplankton biomass in the study lakes were both much higher than expected based on estimates of phytoplankton biomass and models developed for freshwater lakes (i.e. Bird and Kalff 1984; McCauley and Kalff 1981, respectively). Algal populations in the saline lakes were insufficient to support the extremely large zooplankton populations. Consequently, bacteria and abundant detritus are likely an important zooplankton food source in the lakes. Cycling of organic material thus differs from the situation in most freshwater lakes where phytoplankton is a major sourch of food for zooplankton.

This study represents an important advance to our understanding of algal productivity in prairie saline lakes and elucidates ecological differences that exist between freshwater and saline lakes. Typical freshwater relationships between nutrients and productivity, zooplankton and phytoplankton biomass, and bacterial densities and phytoplankton chlorophyll *a* may not be valid for these unique saline systems. As well, analytical techniques which work well on freshwater systems may be unsuitable or require modification in order to be useful for prairie saline waters. This study points to the need for more research on the complex chemical and biological interactions which relate to algal productivity in saline lakes and, to a lesser extent, in all aquatic systems. Specifically, the effects of the high concentrations of Mg^{2+} and SO_4^{2-} on nutrient bio-availability and algal physiology need to be investigated. As well, the trophic relationships between zooplankton, phytoplankton and bacteria in prairie saline lakes need to be

clarified; precise estimates of zooplankton grazing rates on phytoplankton and bacteria should be obtained. The role of the large bacteria populations in nutrient cycling needs quantification. With a clearer understanding of the chemical - biological interactions and the partitioning of energy among communitites in saline lakes, the productivity of prairie saline lakes can be more accurately assessed.

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IV. APPENDIX A: Salinity Gradients in Alberta Saline Lakes

Temporary salinity gradients, or vertical differences in salinity levels, are a common feature of many shallow and highly saline lakes (total dissolved solids - TDS > 5000 $mg\text{-}L^{-1}$) (Beadle 1943; Cohen et al. 1977; Topping and Scudder 1977; Hammer 1978). These salinity gradients result in density gradients, which in turn affect lake stratification since increased energy is required to mix water of different densities (Wetzel 1983). To a large extent, regulation of chemical and biological dynamics in lakes can be influenced by water density differences, there being little movement of water between different density layers. Consequently, the chemical stratification set up by salinity gradients may have important effects on lake productivity and the cycling of material within saline lakes.

The three saline lakes in this Alberta study were all shallow and highly saline; mean depths ranged from 1.3 to 2.1 m while average summer conductivities were 9,400, 13,400 and 55,000 $\mu mhos\text{-}cm^{-1}$ in Fluevog, Peninsula and Oliva Lakes, respectively. The three lakes were sampled from May 1983 to September 1984. For illustrative purposes, results from July 16 and March 18, 1984 were chosen as typical summer and winter data. Profiles compiled in 1983 were similar to those collected in 1984 unless otherwise stated. Due to the shallow depths of the lakes, profiles are represented by only a few points. To investigate possible chemical and thermal stratification in the saline lakes, as well as stratification of phytoplankton populations, vertical profiles of specific conductivity, temperature, dissolved oxygen (DO), phosphorus fractions (total phosphorus; TP, total dissolved phosphorus; TDP, and soluble reactive phosphorus; SRP), and phytoplankton chlorophyll *a* (Chl*a*) were measured. Most profiles were measured at 0.50-m intervals from the lake surface to within 0.70 m from the lake bottom; 1984 summer temperature and conductivity levels in Oliva Lake were measured at 0.25-m intervals. Discrete water samples for the analysis of dissolved oxygen, phosphorus and Chl*a* were collected at three stations with a 1.5-L aluminum drop-sleeve water bottle; the samples were pooled into one sample and laboratory analysis was as described in Chapter 2.

Conductivity and temperature were measured at the main, deep station with a Hydrolab TC-2 metre. To determine if lake conductivity was affected by changes in lake volume, specific conductivity data were also volume weighted over the water column for each sampling date and seasonal variations in conductivity over the open water season were compared to changes in lake depth (measured as the height of a marker stick above the lake surface) or volume.

In all the study lakes, seasonal levels of conductivity and lake depth followed similar patterns (Fig. A1) - as lake volume decreased over the summer and marker height increased, there was a concurrent increase in lake conductivity. However, correlations between conductivity and marker height levels were significant only for Oliva (r = 0.90, n = 14, P = 0.001) and Fluevog Lakes (r = 0.56, n = 12, P = 0.05), and were not significant for Peninsula Lake (r = 0.33, n = 11, P = 0.27). Lack of inflows and outflows in the study lakes would render both conductivity and lake depth highly susceptible to lake evaporation during the summer (June to August) and to ice-melt and run-off dilution during the early spring (May). Peninsula Lake was the largest in volume of the study lakes; lake volumes were calculated as 293, 44 and 68 X 10^4 m^3 for Peninsula, Fluevog and Oliva Lakes, respectively, in August 1983 when the lakes were hand-sounded. The small changes in lake depth (up to 15 cm) observed in all the lakes would therefore have relatively less effect on overall lake volume and the resulting concentration of salts in the larger Peninsula Lake as compared to the other two study lakes - the % maximum lake volume change from the August 1983 volume was 7, 9 and 11% in Peninsula, Fluevog and Oliva Lakes, respectively. As well, slight inaccuracies in conductivity measurements due to limitations of the conductivity probe would lessen the significance of conductivity - marker height relationships. TP, which was measured more accurately in the laboratory (error in TP concentration of ±3% $\mu g \cdot L^{-1}$ from three replicates) showed a more significant relationship with conductivity in all three study lakes (Chapter 2). Seasonal patterns between conductivity and lake depth, attributed to evaporation of small water bodies, have been noted in small aestival ponds in Alberta (White and Hartland-Rowe 1969; Daborn and Clifford 1974) and shallow sloughs in Saskatchewan (Driver and Peden 1977), although the conductivity

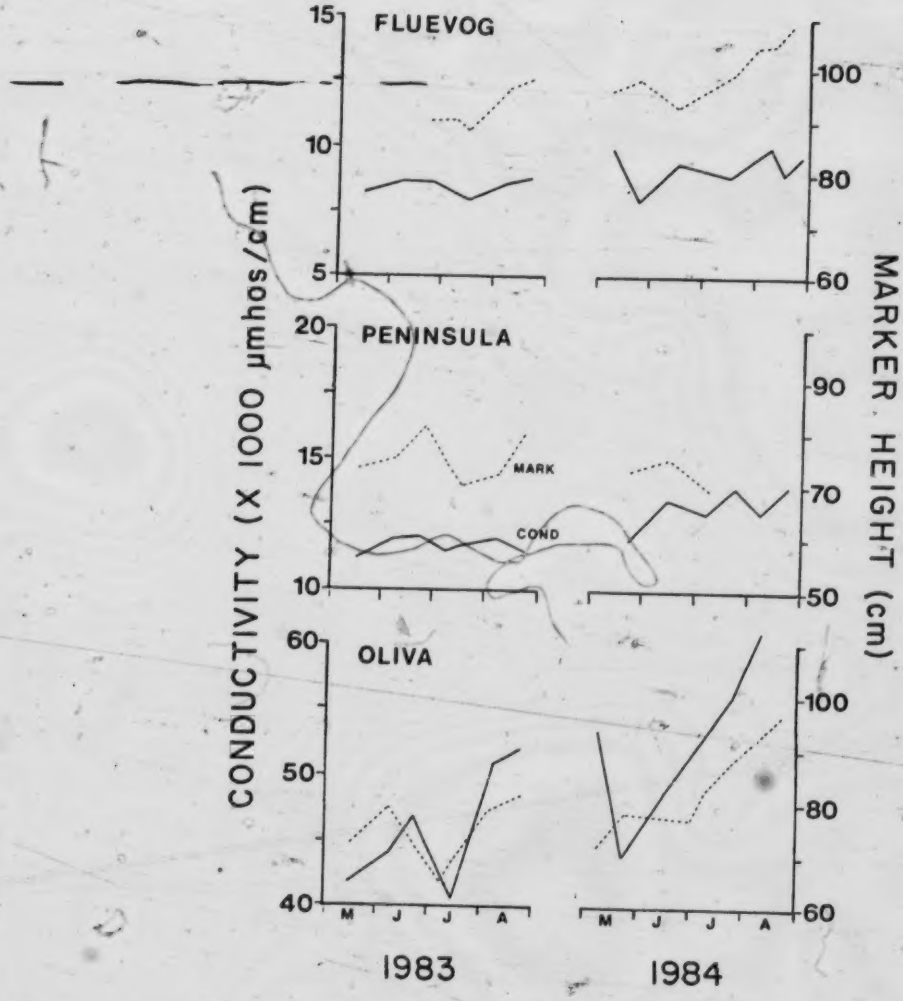

Figure A1: Seasonal variation in specific conductivity (COND, μmhos-cm^{-1}) and marker height (MARK, in cm from the lake surface to the top of a permanent marker stick) for the three saline lakes from May to August 1983 and 1984.

- lake depth correlations were not quantified in any of these studies.

In terms of chemical and thermal stratification, the most saline lake in this study, Oliva Lake, differed noticeably from the less saline Fluevog and Peninsula Lakes. In both Fluevog and Peninsula Lakes, neither temperature nor conductivity were stratified over the summer and winter (Fig. A2a,b). Small differences in temperature and conductivity in these two lakes probably result from sampling artifacts. During the winter, seasonal conductivity increased relative to 1984 summer levels in both lakes, from 9,000 to 11,500 μmhos-cm^{-1} in Fluevog Lake and from 13,000 to 16,000 μmhos-cm^{-1} in Peninsula Lake. In Oliva Lake, both conductivity and temperature were inversely stratified over the summer (Fig. A2c) - conductivity increased from 55,000 μmhos-cm^{-1} at the lake surface to 70,000 μmhos-cm^{-1} at 1.5 m, while temperatures over the sediments ranged from 1 to 2 °C higher than the surface temperatures. Summer stratification in Oliva Lake was completely broken down by strong wind action during the autumn. During the winter, neither conductivity nor temperature were strongly stratified in Oliva Lake; seasonal conductivity levels averaged 55,000 μmhos-cm^{-1} over all depths. Freezing point temperatures in Oliva were depressed below -1 °C. The lowered freezing point of Oliva Lake is a result of interference of the high solute concentration on ice formation, and is typical of saline waters (Hammer and Haynes 1978).

During both winter and summer, there was little stratification of DO levels in either Fluevog or Peninsula Lakes (Fig. A3). In contrast, in Oliva Lake, DO levels were stratified over the summer, but stratification broke down in autumn and winter stratification was weak (Fig. A3). Summer DO levels at the lake surface were slightly less than 8.0 mg-L^{-1} (110% saturation) in both Fluevog and Peninsula Lakes, and were slightly less than 6.0 mg-L^{-1} (110% saturation) in Oliva Lake. Summer DO levels in Oliva Lake decreased noticeably to 3.2 mg-L^{-1} (75% saturation) at 1.5 m. DO levels decreased under ice cover in all the study lakes, to less than 6 mg-L^{-1} (80% saturation) in Fluevog Lake, less than 7.5 mg-L^{-1} (85% saturation) in Peninsula Lake and less than 4.5 mg-L^{-1} (65% saturation) in Oliva Lake. (The % oxygen saturation was determined for specific water temperatures from the tables of Weiss (1970)

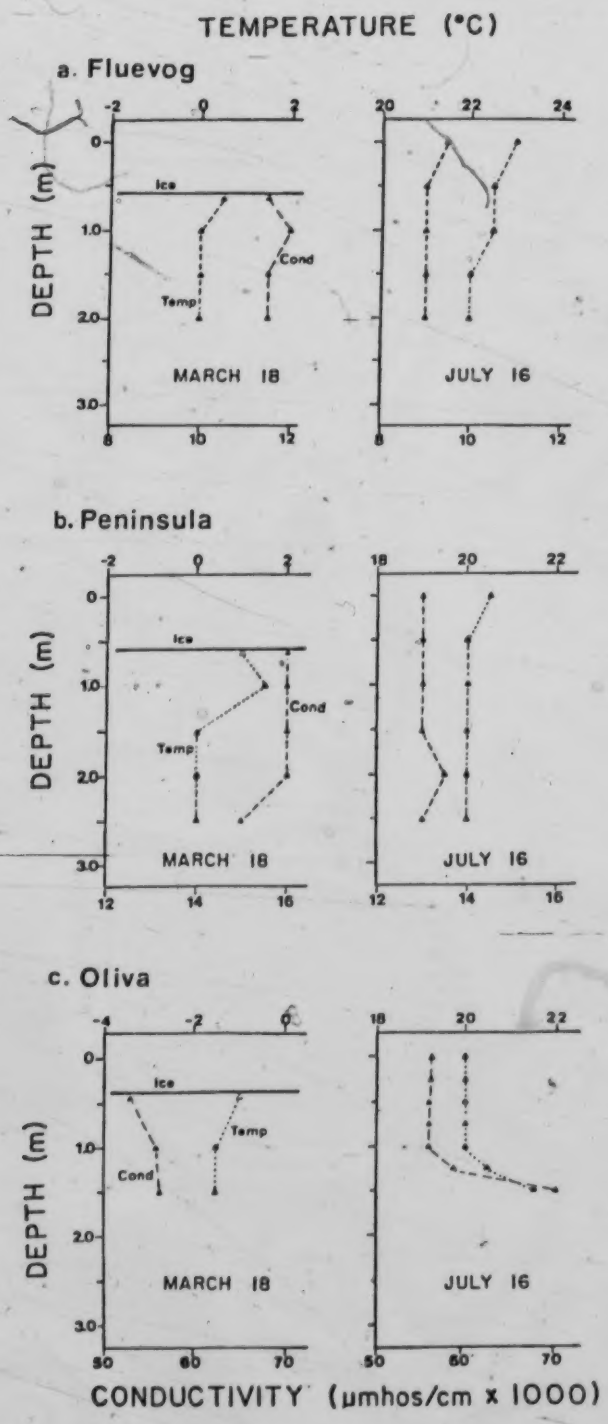

Figure A2: Vertical profiles of specific conductivity (Cond, umhos-cm^{-1}) and temperature (Temp, °C) for the three saline lakes on March 18, 1984 (winter) and July 16, 1984 (summer).

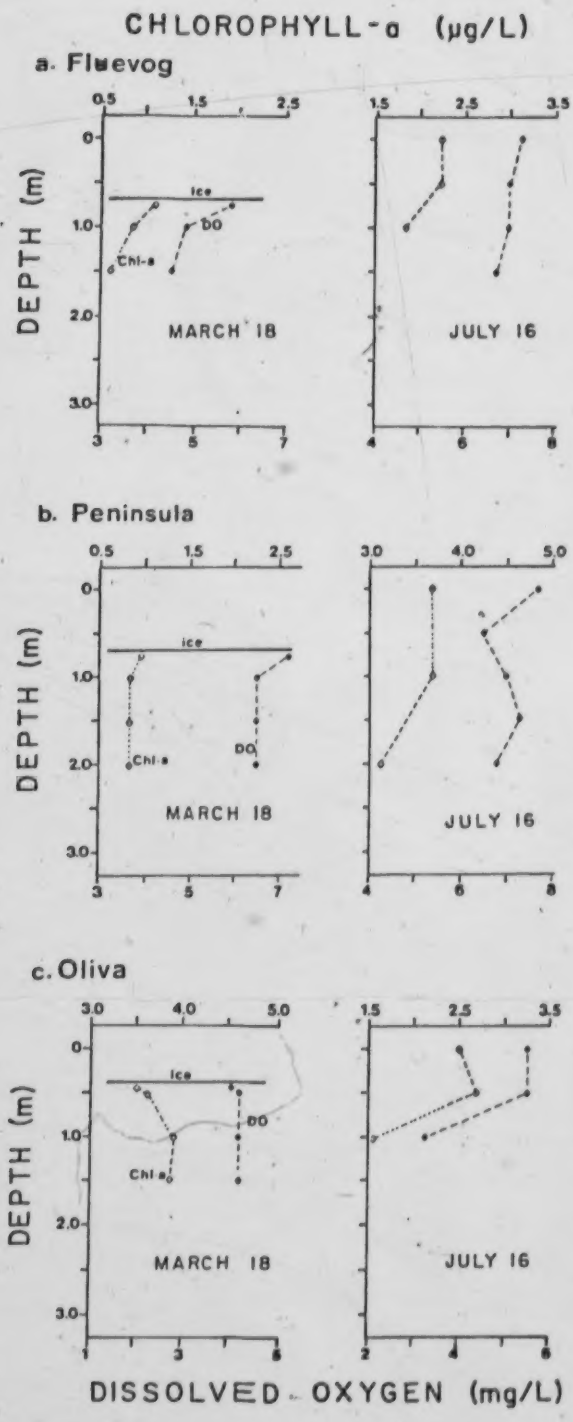

Figure A3: Vertical profiles of phytoplankton chlorophyll *a* (Chl*a*, µg-L^{-1}) and dissolved oxygen (DO, mg-L^{-1}) for the three saline lakes on March 18, 1984 (winter) and July 16, 1984 (summer).

corrected for salinity, with Mortimer's corrections for elevation from Hutchinson 1957). Thus, the lakes were never anoxic.

TP levels also remained unstratified over the year in Fluevog and Peninsula Lakes, but were strongly stratified during the summer in Oliva Lake (Fig. A4). In Fluevog and Peninsula Lakes, summer TP levels at the lake surface were 2,400 and 3,750 $ug\text{-}L^{-1}$ and winter TP levels at the lake surface increased to 3,000 and 4,500 $ug\text{-}L^{-1}$, respectively. Summer TP levels in Oliva Lake averaged 14,200 $ug\text{-}L^{-1}$ at the lake surface and increased to 15,200 $ug\text{-}L^{-1}$ at 1.5 m. Summer TP stratification was broken down by autumn wind action. In winter, TP levels in Oliva Lake were homogeneous throughout the water column and averaged 16,000 $ug\text{-}L^{-1}$. In all the lakes, TDP and SRP levels followed patterns similar to TP levels, with $>$ 90% of summer TP in the dissolved fraction (TDP) and $>$ 80% of summer TP present as SRP (Fig. A4).

Summer Chl*a* levels in all the lakes were most abundant in the top 0.50 to 0.75 m of the water column with surface levels of 2.1, 3.6 and 2.5 $ug\text{-}L^{-1}$ in Fluevog, Peninsula and Oliva Lakes, respectively (Fig. A3). In summer, the trophogenic zones extended to 0.6, 0.8 and 1.6 m on average in Fluevog, Peninsula and Oliva Lakes, respectively; Chl*a* was seemingly limited by light availability (i.e. the bottom of the trophogenic zone) only in Fluevog and Peninsula Lakes. In winter, Chl*a* levels were generally unstratified in all the lakes; surface levels decreased from summer values to 1.0 $ug\text{-}L^{-1}$ in Fluevog and Peninsula Lakes and increased from summer values to 3.5 $ug\text{-}L^{-1}$ in Oliva Lake.

The uniform vertical distributions of specific conductivity, temperature, DO and phosphorus levels in both Fluevog and Peninsula Lakes are similar to shallow and less saline lakes in the area (J. A. Bierhuizen, University of Alberta, *unpubl.*) and to lakes of similar salinity in other parts of western Canada (Driver 1965 in Manitoba; Hammer and Haynes 1978 in Saskatchewan). Since Fluevog and Peninsula Lakes are shallow and average wind speeds in the area are moderate (13 $km\text{-}h^{-1}$; Environment Canada 1984), summer stratification is unlikely. In contrast, the more saline Oliva Lake exhibited strong inverse stratification over the summer. The higher salinity of Oliva Lake water allows for development of temporary salinity

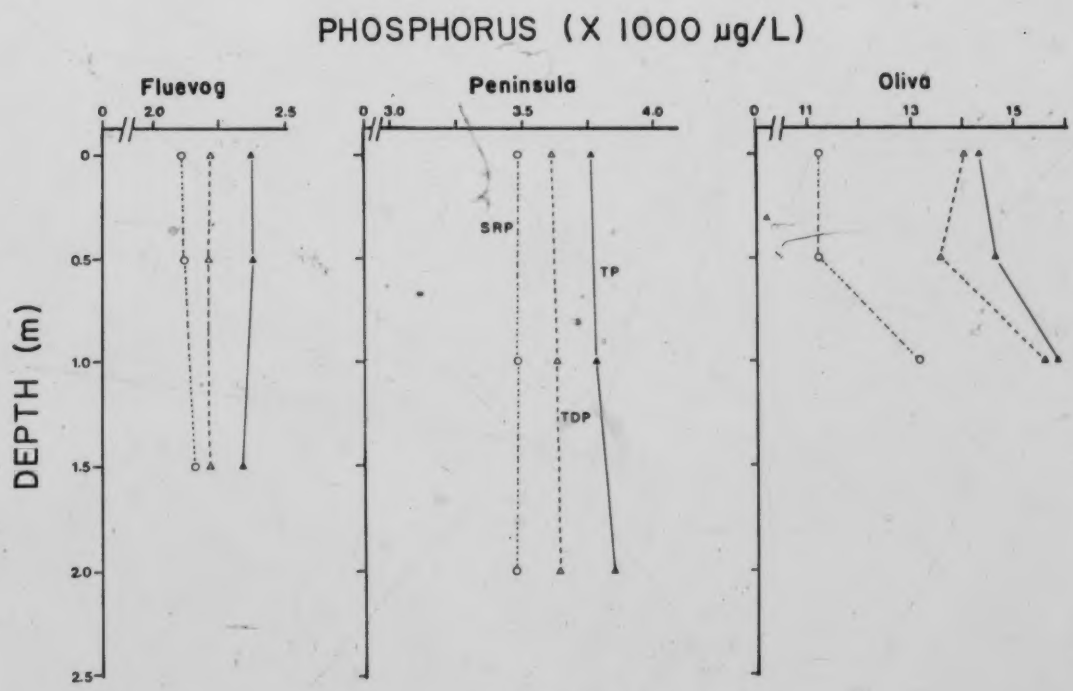

Figure A4: Vertical profiles of phosphorus ($\mu g \cdot L^{-1}$) as total phosphorus (TP), total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) for the three saline lakes on July 16, 1984 (summer).

gradients strong enough to resist summer wind action and mixing events. The summer density gradient forms primarily as a result of freeze out of salts from the ice (Daborn and Clifford 1974; Canfield et al. 1983) at the end of the previous winter. These salts sink down to the sediments to form a bottom layer of salt clearly visible at ice off (*pers. obs.*), while spring meltwater produces a more dilute surface layer. As a result of initial wind mixing in the spring, the bottom salts are partially resuspended in solution. The relatively more saline bottom waters would then remain unmixed with the rest of the water column. Establishment of the salinity gradient allows for development of an inverse thermal gradient. Since saline waters are practically opaque to infra-red rays (Sonnenfield and Hudec 1980), radiant energy of the sun is partially trapped in the highly saline bottom waters with negligible release of heat from water column circulation. Permanent cases of inverse thermal gradients have been reported in meromictic saline lakes (Beadle 1943; Anderson 1958; Hammer et al. 1978; Burton 1981). In Oliva Lake, increased wind action and decreased temperatures in autumn would lead to the breakdown of the salinity gradient and the subsequent overturn of the lake.

Summer stratification of DO and phosphorus in Oliva Lake was probably a direct result of the temporary salinity gradient that prevented lake mixing, and thus restricted movements of oxygen into, and movements of phosphorus out of, the bottom waters of the lake. Calculated phosphorus sedimentation (fresh water sedimentation rates of 1.5% of summer TP from the trophogenic zone per day; Rigler 1973) could account for a large proportion (80 to 90%) of the increase in phosphorus levels at 1.5 m. Such calculations assume that biological sedimentation rates from productive freshwater systems are applicable to Oliva Lake. However, this assumption is unreasonable given the low algal biomass relative to high phosphorus levels in the trophogenic zone that are observed in Oliva Lake (Chapter 2).

Temporary inverse stratification in the summer is not uncommon in shallow lakes with salinities similar to Oliva Lake. In a study of saline lakes in central British Columbia, Topping and Scudder (1977) observed temporary inverse chemical and thermal stratification in lakes with mean depths < 3 to 4 m and conductivities $> 5{,}000$ μmhos-cm^{-1}. Little Manito Lake

(TDS 95,000 mg-L^{-1}) in Saskatchewan exhibited almost permanent inverse stratification although the strong chemocline was overcome by autumn wind action (Hammer 1978), as was the case in Oliva Lake. Solar Lake, Sinai, a brine filled basin (TDS 180,000 mg-L^{-1}) shielded from the wind, also exhibited strong inverse stratification, yet with a brief period of overturn in July and September (Cohen et al. 1977). In Solar Lake, the salinity gradient was created through salt water seepage into the bottom of the basin; the gradient was destroyed when high surface evaporation rates were able to compensate for the salt water input (Cohen et al. 1977).

High salinity combined with mean depths < 5 m in many saline lakes thus allows for the development of a salinity gradient in summer, as in Oliva Lake, but a gradient that is finally not strong enough to resist autumn wind action. These lakes consequently are not permanently meromictic. Salinity levels in Fluevog and Peninsula Lakes are not high enough to set up an initial salinity gradient and freeze out of salts in winter is not pronounced. Alternatively, lake basin topography may influence the development of a salinity gradient. Saline lakes that are in unsheltered basins and open to the mixing action of wind are less likely to develop salinity gradients than are saline lakes in more sheltered basins (examples being unstratified Green Lake v.s. stratified Mahoney Lake; Northcote and Hall 1983). Fluevog and Peninsula Lakes appeared more affected by summer wind action than did Oliva Lake (pers. obs.) - Oliva Lake was situated in a relatively sheltered basin, while Fluevog and Peninsula Lakes were in more open terrain. Salinity level, mean depth and topography therefore will all influence the development of a temporary salinity gradient.

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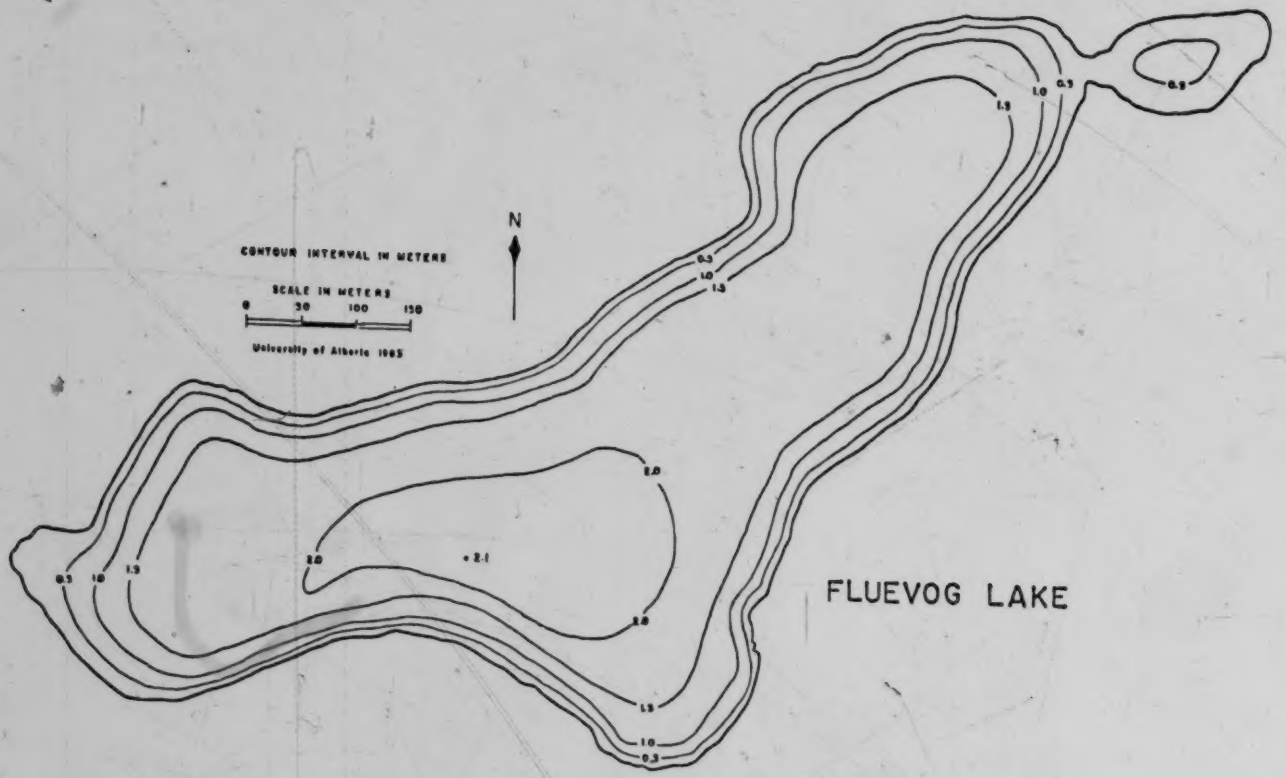
V. APPENDIX B: Morphometric maps of the three saline lakes


CONTOUR INTERVAL IN METERS
SCALE IN METERS
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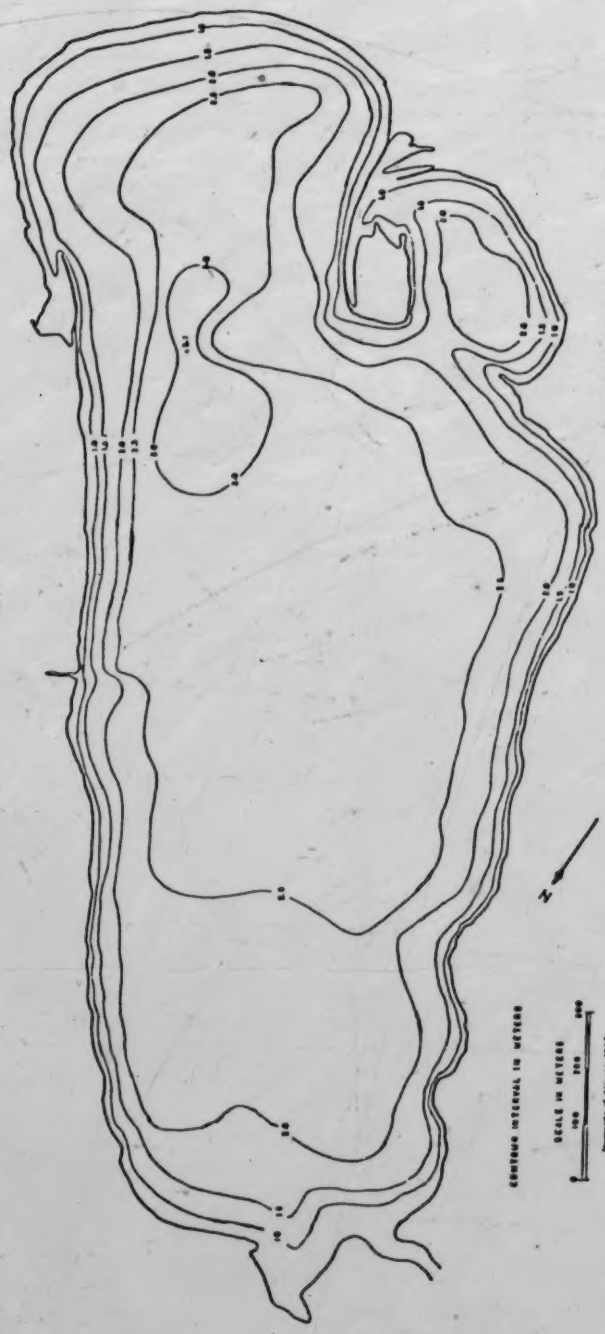
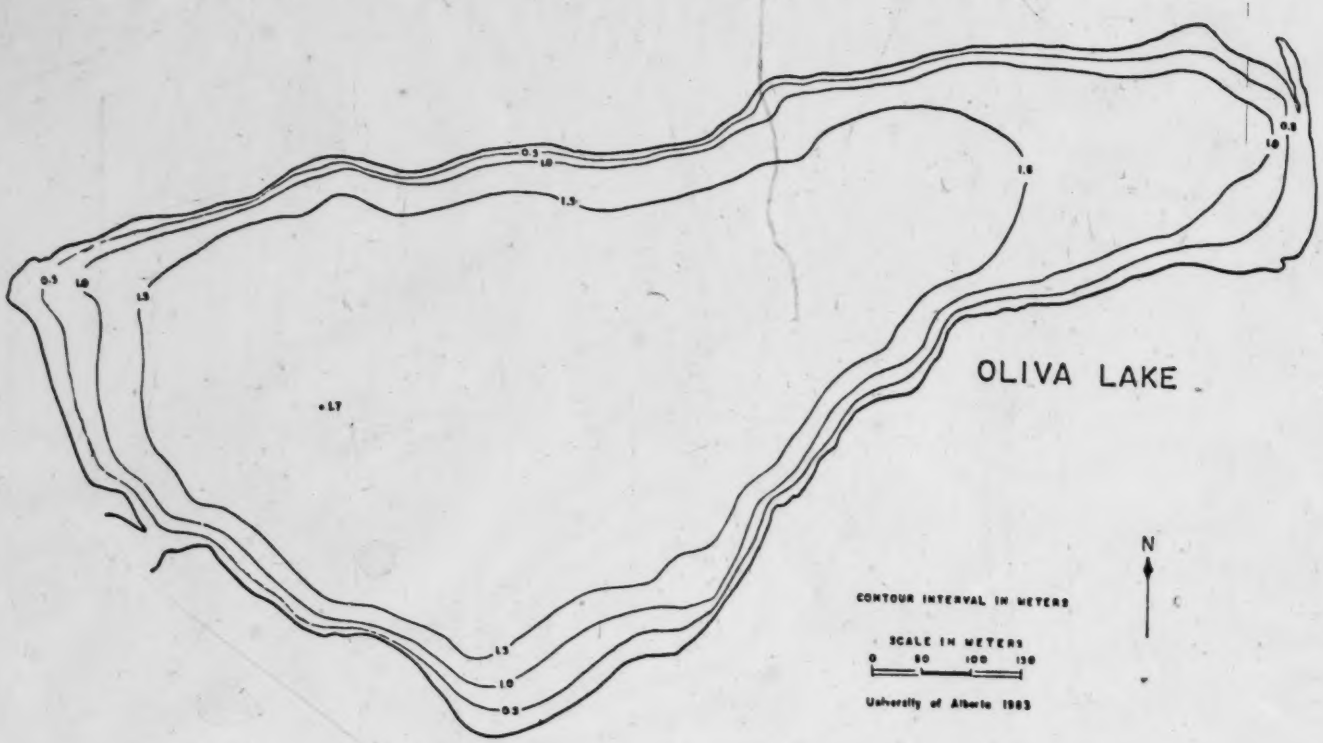
University of Alberta 1985
N
0.3
1.0
1.5
2.0
2.1
FLUEVOG LAKE


PENINSULA LAKE
N


0.5
1.0
1.5
0.5
1.0
1.5
1.0
0.5
1.0
1.0
1.7
OLIVA LAKE
N
CONTOUR INTERVAL IN METERS
SCALE IN METERS
0 50 100 150
University of Alberta 1983

VI. APPENDIX C: Seasonal variation of phytoplankton chlorophyll, total phosphorus and specific conductivity in the three saline lakes

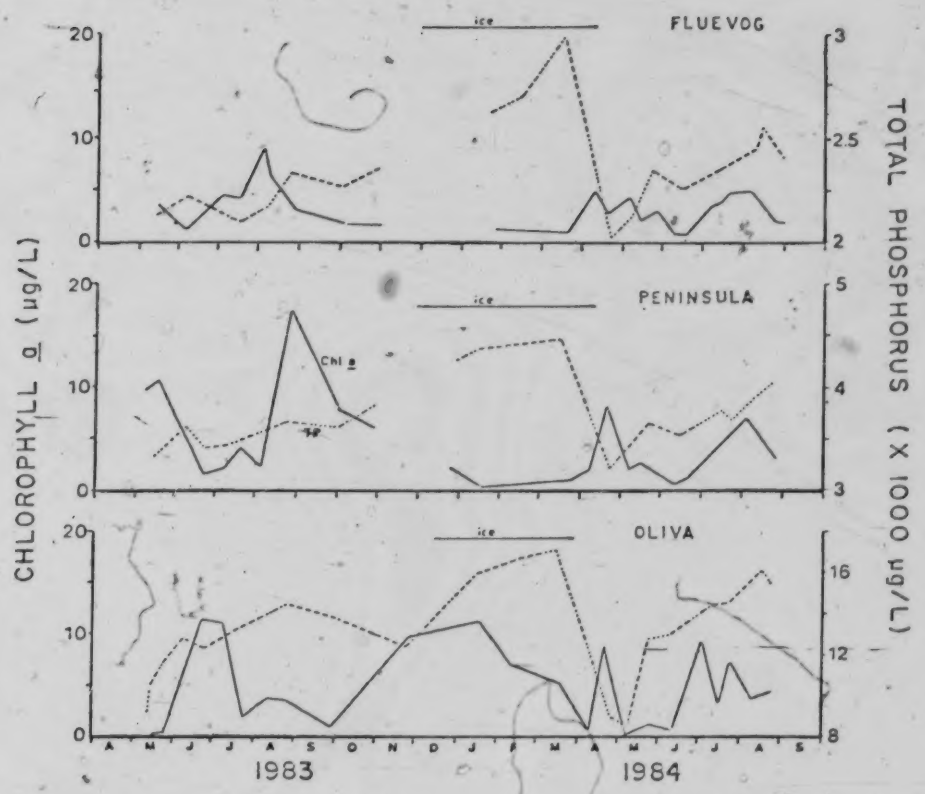


Figure C1: Seasonal variation in both phytoplankton chlorophyll (Chl*a*, $\mu g \cdot L^{-1}$) and total phosphorus (TP, $\mu g \cdot L^{-1}$) in the trophogenic zone for the three saline lakes in 1983 and 1984.

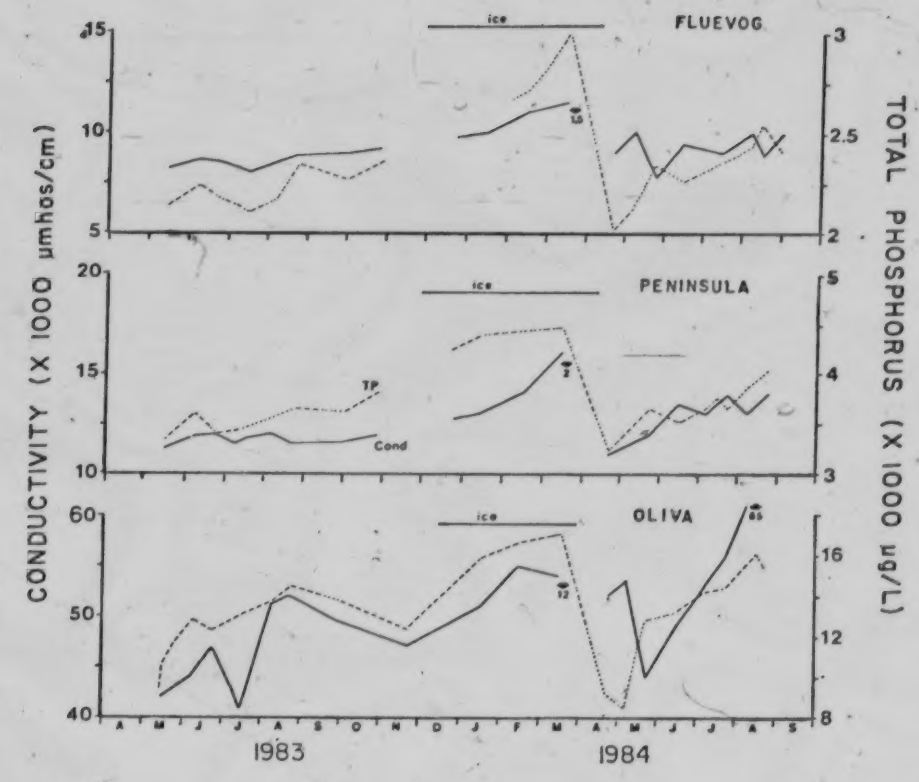


Figure C2: Seasonal variation in specific conductivity (Cond, umhos-cm^{-1}) volume weighted over the water column and total phosphorus (TP, ug-L^{-1}) in the trophogenic zone for the three saline lakes in 1983 and 1984.

VII. APPENDIX D: Regression equations used in thesis

Table D1: Regression equations from the literature. (Values in brackets refer to range of variables in equations). Variables are as follows:

Chl*a* = mean growing season chlorophyll *a* in the trophogenic zone; $ug\text{-}L^{-1}$

TP = mean growing season total phosphorus in the trophogenic zone; $ug\text{-}L^{-1}$

TN = mean growing season total nitrogen in the trophogenic zone; $ug\text{-}L^{-1}$

V = mean growing season primary productivity in the trophogenic zone; $mg\ C\text{-}m^{-3}\text{-}d^{-1}$

Zoop = mean growing season zooplankton wet weight at 1 m below lake surface; $mg\text{-}L^{-1}$

Phyto = mean growing season phytoplankton volume in the tropogenic zone; $ug\text{-}L^{-1}$

Bact = mean summer bacteria densities at 1 m below lake surface; $cells\text{-}mL^{-1}$

Chla^1 = mean summer chlorophyll *a* in the trophogenic zone; $ug\text{-}L^{-1}$

1. $\log_{10}Chla = 0.653\log_{10}TP + 0.548\log_{10}TN - 1.517, \quad r^2 = 0.76$ Smith (1982)

   (Chl*a* from 0 to 200, TP from 1 to 1500, TN from 0 to 5000)

2. $V = 10.4TP - 79, \quad r^2 = 0.94$ Smith (1979)

   (V from 0 to 2000, TP from 0 to 200)

3. $V = 22.9Chla - 42.6, \quad r^2 = 0.81$ Smith (1979)

   (V from 0 to 2000, Chl*a* from 0 to 80)

4. $\log_{10}Zoop = 0.719\log_{10}Phyto + 1.01, \quad r^2 = 0.74$ McCauley and Kalff (1981)

   (Zoop from 1 to 5, Phyto from 1 to 5)

5. $\log_{10}Bact = 0.776\log_{10}Chla^1 + 5.867, \quad r^2 = 0.88$ Bird and Kalff (1984)

   (Bact from 10^5 to 10^8, Chla^1 from 0 to 100)

VIII. APPENDIX E: Chemical and biological data for the three saline lakes

Table E1: 1983 and 1984 chemical and biological data for the three saline study lakes. Variables are defined as follows:

D = day
M = month
Y = year
Mark = marker height (cm above lake surface)
Cond = specific conductivity (μmhos-cm^{-1}, integrated over the water column)
TP = total phosphorus (μg-L^{-1}, integrated over the trophogenic zone)
TDP = total dissolved phosphorus < 0.45 μm (μg-L^{-1}, integrated over the trophogenic zone)
TDP<0.2 = total dissolved phosphorus < 0.20 μm (μg-L^{-1}, integrated over the trophogenic zone)
Chl = phytoplankton chlorophyll *a* (μg-L^{-1}, integrated over the trophogenic zone)
Zoop = zooplankton dry weight biomass (mg-L^{-1} from 1 m)
Turb = turbidity (NTU units)
Col = colour (Pt mg-L^{-1}, measured with the platinum-cobalt method on an Hellige-Aqua tester Model 611-A)
TN = total nitrogen[1] (μg-L^{-1}, integrated over the trophogenic zone)
NO2-NO3 = nitrate-nitrite[1] (μg-L^{-1}, integrated over the trophogenic zone)
NH4-N = ammonia[1] (μg-L^{-1}, integrated over the trophogenic zone)
Alk = alkalinity ($CaCO_3$ mg-L^{-1})
SD = Secchi disc reading (m)

([1]: analyzed by J. Bierhuizen and G. Hutchinson in 1983 and by F. Parkinson and G. Hutchinson in 1984)

Table E1 (continued)

Lake	D	M	Y	Mark	Cond	TP	TDP	TDP<0.2	Chl	Zoop	Turb	Col	TN	NO2-NO3	NH4-N	Alk	pH	SD
Fluevog																		
	17	05	83		8268	2131	2094		3.3		18.0	100	3970	21.5	58.4			0.50
	06	06	83		8640	2230	2111		1.5		17.0	90	4012	64.6	101.2			0.80
	20	06	83	0.90	8575	2165	2006		2.7	0.77	19.0	100	4091	93.7	59.8	2080	9.20	0.55
	06	07	83	0.90	8200	2118	1969		4.7	0.56	17.0	100				2180	9.16	0.65
	19	07	83	0.88	8000	2103	2011		3.6	1.38	16.0	80	5089	26.4	21.0	2080	9.15	0.60
	11	08	83	0.96	8550	2171	2064		6.5	1.59	14.0	80	3930	1.2	40.0	2140	9.19	0.50
	28	08	83	0.98	8750	2336	2266		3.3	0.79	9.5	100	5081	5.3		2234	9.19	1.05
	01	10	83	1.00	8850	2261	2150		2.2	1.04	11.5	80				2200	9.22	0.70
	13	02	84		11000					0.42	4.3	110						
	18	03	84		11500					1.36								
	09	04	84		10000													
	20	04	84		10500					0.46								1.00
	07	05	84		10000	2118	2025		4.5	2.80								0.65
	16	05	84	0.96	9500	2149	2015		2.4	1.72						2060	9.17	0.50
	30	05	84	0.98	8000	2331	2116	2171	3.6	1.75						2120	9.18	0.60
	11	06	84		9500	2248	2091		0.9	1.29								0.80
	20	06	84	0.93	9500	2192	1996		1.1	1.03			3688	17.3		2060	9.21	0.70
	05	07	84	0.99	9000	2260	2111	2064	3.8	0.52						2090	9.31	0.60
	18	07	84		9000	2366	2215		4.0	1.60			3940	79.4				0.60
	25	07	84	1.04	9500	2351	2157		5.1	1.01						2160	9.15	0.70
	09	08	84	1.05	10000	2447	2187	2260	5.5	1.11						2310	9.18	0.60
	22	08	84	1.09	9000	2550	2355		2.2	0.89						2290	9.11	0.60
	29	08	84		10000	2550	2295		2.3	1.10			4144	57.4				0.80
Peninsula																		
	11	05	83	0.72	11250	3323	3233		10.0	0.57	9.0	40				2150	9.19	0.50
	19	05	83	0.75	11100	3592	3316		11.0	1.11	8.3	40	4607	3.4	24.3	2140	9.25	0.50
	07	06	83	0.81	11950	3625	3405		6.8	1.05	14.5	50				2220	9.23	0.60
	21	06	83	0.74	12000	3399	3247		2.0	2.21	17.0	50	4809	51.4	100.3	2185	9.25	0.70
	07	07	83	0.70	11500	3420	3220		2.3	1.10	12.5	50				2170	9.20	1.05
	20	07	83	0.72	11750	3438	3301		4.3	0.94	14.0	45	5251	83.9	38.4	2170	9.21	0.75
	12	08	83	0.80	12000	3385	3270		3.6	1.31	13.5	45	4382	15.5	45.8	2200	9.22	0.70
	27	08	83	0.83	11450	3662	3528		17.9	3.81	10.5	45	4341	0.6		2092	9.25	1.15
	01	10	83	0.87	11600	3612	3497		8.2	0.64	11.5	45				2250	9.23	0.75
	17	01	84		12500					0.67	3.0	40						
	13	02	84		13900					1.65	2.6	40						
	18	03	84		16000					2.65								
	20	04	84		11000					0.66								1.30
	07	05	84		14000	3326	3239		2.6	1.43								1.30

Table E1 (continued)

Lake	D	M	Y	Mark	Cond	TP	TDP	TDP<0.2	Chl	Zoop	Turb	Col	TN	NO3-NO3	NH4-N	Alk	pH	SD
	15	05	84	0.73	13900	3439	3324		2.6	1.98						2190	9.27	1.60
	29	05	84	0.75	12000	3649	3443	3565	2.4	2.03						2230	9.22	1.20
	11	06	84		13500	3553	3378		0.5	1.11								1.10
	19	06	84	0.70	13000	3512	3271		1.2	1.52			3487	6.6		2150	9.26	1.10
	04	07	84		13000	3679	3223	3280	3.3	1.23						2215	9.12	0.90
	16	07	84		13000	3756	3609		4.3	1.27			4340	86.8				0.80
	24	07	84	0.79	13000	3638	3544		84.5	1.17						2270	9.25	0.60
	08	08	84		14000	3867	3639	3726	7.3	0.89						2550	9.16	0.80
	21	08	84		14000	4034	3883		3.7	1.70						2430	9.13	0.90
	27	08	84		14000	3785	3673		3.8	1.53			4707	165.8				1.50
Oliva																		
	14	05	83		42000	10519	10214		0.3	8.30	1.9	20	5626	0.0	233.2	22900	9.95	1.50
	22	05	83	0.72	42750	11498	11090		0.4	7.65	1.5	25				24100	9.99	1.60
	10	06	83	0.79	44000	12806	12466		4.6	4.26	1.4	25	8396	0.0	443.9	25200	9.94	1.50
	22	06	83	0.72	46000	12316	11834		11.6	16.65	1.9	30	9599	0.0	592.0	26900	9.97	1.60
	08	07	83	0.65	43000	12875	11868		11.1		3.0	35				22850	9.98	1.50
	21	07	83	0.69	40500	12940	12591		1.5		3.0	30	11849	11.7	216.7	25000	9.89	1.40
	10	08	83	0.78	51500	13628	13202		3.9	4.37	2.6	30	11759	0.0	392.5	27200	9.89	1.60
	29	08	83	0.81	52250	14530	14465		3.5	6.91	2.0	30	12085	0.8		29440	9.86	1.50
	01	10	83	0.87	49500	13840	13545		0.8	4.40	2.5					29000	9.87	1.65
	23	11	83		47000													
	17	01	84		51000					0.49	1.2	40						
	13	02	84		50250					2.28	0.8	40						
	18	03	84		53500					2.95								
	20	04	84		54000													1.00
	07	05	84	0.78		8534	8370		0.1	4.91						18100	9.99	1.60
	14	05	84	0.72	41000	9900	9625		0.6									1.50
	28	05	84	0.78	49500	12808	12683	12246	1.7	12.75						22900	9.83	1.60
	11	06	84		45000	13173	12478		0.7	12.14								1.65
	18	06	84	0.77	49000	13173	12148		7.2	13.21			9489	0.0		22800	9.90	1.70
	03	07	84	0.82	53000	14375	13200	13087	11.1	8.94						23200	9.90	1.60
	16	07	84		56000	14315	14078		2.8	7.89			12491	0.0				1.65
	23	07	84	0.88	56000	14370	13623		8.2	5.94						21000	9.97	1.60
	07	08	84	0.92	58000	14635	14133	14605	3.9	6.89						25000	9.86	1.50
	20	08	84	0.97	61000	16125	15243		4.5	5.12						26000	9.79	1.50
	27	08	84		65000	15383	15133		2.5	4.17			12567	0.0				1.60

Table E2: 1983 and 1984 vertical profiles of chemical and biological data for the three saline study lakes. Variables are defined as follows:

D = day
M = month
Y = year
Depth = depth of sample (m)
Temp = temperature (° C)
Cond = specific conductivity (μmhos-cm^{-1})
TP = total phosphorus (μg-L^{-1})
TDP = total dissolved phosphorus (μg-L^{-1})
SRP = soluble reactive phosphorus (μg-L^{-1})
Chl = phytoplankton chlorophyll *a* (μg-L^{-1})
DO = dissolved oxygen (mg-L^{-1})

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
Fluevog											
	17	05	83	0	12.0						
				1.0	12.0						
				2.0							
	06	06	83	0	16.5						
				1.0	16.5						
				2.0							
	20	06	83	0	15.0						
				0.5	15.0						
				1.0	14.5						
				1.5	14.5						
				2.0	14.5						
	06	06	83	0	23.0						
				0.5	22.5						
				1.0	22.0						
				1.5	21.0						
				2.0	19.0						
	19	07	83	0	23.0						
				0.5	22.0						
				1.0	22.0						
				1.5	22.0						
				2.0	21.0						
	28	08	83	0	18.5						
				0.5	18.5						
				1.0	18.5						
				1.5	18.5						
				2.0	18.0						
	01	10	83	0	7.5						
				0.5	7.5						
				1.0	7.5						
				1.5	7.5						
				2.0	8.0						
	13	02	84	0	0.5						
				0.5	0.0						
				1.0	0.0		2710	2626		0.5	
				1.5	0.0						
				2.0							
	18	03	84	0	0.5		3000	2795		1.2	5.4
				0.5	0.5						5.8
				1.0	0.5		3000	2880		0.8	4.8
				1.5	0.0		3151	2914		0.5	4.4

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				2.0	0.0						
	20	04	84	0	12.0	9000					7.5
				0.5	12.0	9000					
				1.0	11.5	9000					
				1.5	11.0	11000					6.3
				2.0	8.0	12000					
	07	05	84	0	11.0	10000	2118	2025		4.5	8.7
				0.5	11.0	10000	2078	1835		3.3	9.3
				1.0	11.0	10000				4.5	8.2
				1.5	11.0	10000	2078	1970			8.6
				2.0	10.5	10000					
	16	05	84	0	14.0	9500					
				0.5	14.0	10000					
				1.0	14.0	10000					
				1.5	14.0	10000					
				2.0	14.0	10000					
	30	05	84	0	16.0	8000					
				0.5	16.0	8000					
				1.0	16.0	8000					
				1.5	15.5	8000					
				2.0							
	11	06	84	0	17.0	9500	2248	2091	1972	1.0	7.0
				0.5	15.5	9500	2184	2085	2032	0.9	6.9
				1.0	14.0	9500				1.1	7.0
				1.5	13.5	9500	2233	2036	1994		6.9
				2.0	13.0	9500					
	20	06	84	0	17.5	9500					
				0.5	17.5	9500					
				1.0	17.5	9500					
				1.5	17.5	9500					
				2.0	17.5	9500					
	05	07	84	0	20.0	8500					
				0.5	19.5	9000					
				1.0	19.0	9500					
				1.5	19.0	9500					
				2.0	19.0	9500					
	16	07	84	0	24.0	9500	2366	2215	2110	4.0	7.4
				0.5	23.0	9000	2378	2212	2114	3.5	7.0
				1.0	22.5	9000				4.5	7.0
				1.5	22.0	9000	2342	2223	2160		6.7

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				2.0	21.0	9000					
	25	07	84	0	21.5	9000					
				0.5	21.0	9500					
				1.0	22.0	9500					
				1.5	20.0	10000					
				2.0	19.5	10000					
	09	08	84	0	12.0	9000					
				0.5	22.0	10000					
				1.0	21.5	10000					
				1.5	21.5	10000					
				2.0	21.5	10000					
	22	08	84	0	17.5	9000					
				0.5	17.5	9000					
				1.0	17.5	9000					
				1.5	17.5	9000					
				2.0	17.5	9000					
	27	08	84	0	20.0	10500	2400	2295	2562	2.3	6.6
				0.5	20.0	10000	2422	2318	2475	2.3	6.4
				1.0	20.0	10000				1.9	7.0
				1.5	20.0	10000	2421	2336	2526		6.7
Peninsula											
	11	05	83	0	10.0						
				0.5	9.5						
				1.0	9.0						
				1.5	9.0						
				2.0	9.0						
				2.5	9.0						
				3.0	9.0						
	19	05	83	0	12.5						
				0.5	12.5						
				2.0	12.5						
				1.5	12.5						
				2.0	12.0						
				2.5	12.0						
	07	06	83	0	16.5						
				0.5	16.5						
				1.0	16.5						
				1.5	16.5						
				2.0	16.5						

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				2.5	16.5						
				3.0	16.5						
	21	06	83	0	15.0						
				0.5	15.0						
				1.0	15.0						
				1.5	15.0						
				2.0	15.0						
				2.5	15.0						
				3.0	15.0						
	07	07	83	0	22.0						
				0.5	22.0						
				1.0	22.0						
				1.5	21.5						
				2.0	21.0						
				2.5	19.5						
	20	07	83	0	22.0						
				0.5	22.0						
				1.0	22.0						
				1.5	22.0						
				2.0	22.0						
				2.5	22.0						
				3.0	22.0						
	27	08	83	0	18.0						
				0.5	18.0						
				1.0	18.0						
				1.5	18.0						
				2.0	18.0						
				2.5	18.0						
	01	10	83	0	9.0						
				0.5	9.0						
				1.0	9.0						
				1.5	9.0						
				2.0	9.0						
				2.5	9.0						
	17	01	84	0	0.5					0.5	
				0.5	1.0						
				1.0	1.0		4390	4245			
				1.5	1.0						
				2.0	1.0						

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
	13	02	84	0	0.5						
				0.5	0.5						
				1.0	0.5		4470	4407		0.3	
				1.5	0.5						
				2.0	0.5						
	18	03	84	0	1.0	16000	4435	4376		0.7	6.1
				0.5	0.5	17000					7.2
				1.0	0.5	16000	4694	4548		0.6	6.5
				1.5	0.0	16000					6.6
				2.0	0.0	16000	4668	4504		0.6	6.5
				2.5	0.0	16000					
	20	04	84	0	10.0	11000					9.1
				0.5	9.0	11000					
				1.0	9.0	11000					9.1
				1.5	9.0	11000					
				2.0	9.0	11000					9.1
				2.5	8.5	11000					
	07	05	84	0	9.0	14000	3326	3239		2.6	9.3
				0.5	9.0	14000					9.1
				1.0	9.0	14000	3322	3297		2.7	8.5
				1.5	9.0	14000					9.0
				2.0	9.0	14000	3584	3381		2.2	8.5
				2.5	9.0	14000					
				3.0	9.0	14000					
	15	05	84	0	12.5	14000					
				0.5	12.0	13900					
				1.0	12.0	13900					
				1.5	12.0	13900					
				2.0	12.0	13900					
				2.5	12.0	13900					
				3.0	12.0	13900					
	29	05	84	0	15.0	12000					
				0.5	14.5	12000					
				1.0	14.0	12000					
				1.5	13.0	12000					
				2.0	13.0	12000					
				2.0	13.0	12000					
				2.5	13.0	12000					
	11	06	84	0	15.5	13000	3553	3378	3340	0.6	7.2
				0.5	15.0	13500					7.0

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				1.0	14.5	13500	3527	3333	3335	0.7	7.0
				1.5	14.0	13500					6.7
				2.0	14.0	13500	3620	3464	3390	0.9	7.4
				2.5	13.5	13500					
	19	06	84	0	17.5	12000					
				0.5	17.5	13000					
				1.0	17.5	13000					
				1.5	17.5	13000					
				2.0	17.0	13000					
				2.5	17.0	13000					
	04	07	84	0	19.0	13000					
				0.5	18.5	13000					
				1.0	18.5	13000					
				1.5	18.5	13000					
				2.0	18.5	13000					
				2.5	18.5	13000					
	16	07	84	0	20.0	13000	3756	3609	3479	4.6	7.6
				0.5	20.0	13000					6.5
				1.0	20.0	13000	3786	3633	3447	3.6	7.1
				1.5	20.0	13000					7.4
				2.0	20.0	13500	3844	3628	3466	3.6	6.8
				2.5	20.0	13000					
	24	07	84	0	19.5	14000					
				0.5	19.5	14000					
				1.0	19.5	14000					
				1.5	19.5	14500					
				2.0	19.0	14500					
				2.5	18.0	14500					
	08	08	84	0	21.0	14000					
				0.5	20.5	14000					
				1.0	20.5	14000					
				1.5	20.5	14000					
				2.0	20.5	14000					
				2.5	20.5	14000					
	21	08	84	0	17.0	13000					
				0.5	17.5	13000					
				1.0	17.5	14000					
				1.5	17.5	14000					
				2.0	17.5	14000					
				2.5	17.5	14000					

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
	27	08	84	0	19.5	14000	3785	3673	3994	3.8	7.0
				0.5	19.5	14000					6.9
				1.0	19.5	14000	3783	3721	3952	3.6	7.1
				1.5	19.5	14000					7.4
				2.0	19.5	14000	3794	3657	3902	3.2	6.7
				2.5	19.5	14000					
Oliva											
	14	05	83	0	11.0						
				0.5	11.0						
				1.0	17.0						
				1.5	16.0						
	22	05	83	0	14.0						
				0.5	14.0						
				1.0	16.5						
				1.5	17.0						
	10	06	83	0	21.0						
				0.5	21.0						
				1.0	22.0						
				1.5	22.0						
	22	06	83	0	16.0						
				0.5	16.0						
				1.0	16.0						
				1.5	16.0						
	21	07	83	0	23.0						
				0.5	23.0						
				1.0	23.0						
				1.5	23.0						
	29	08	83	0	18.0						
				0.5	18.0						
				1.0	18.0						
				1.5	20.0						
	01	10	83	0	8.0						
				0.5	8.0						
				1.0	8.0						
				1.5	8.0						
	17	01	84	0	-1.0		15785	15600		10.8	
				0.5	-1.0						
				1.0	-1.0		15765	15205		11.8	

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
	13	02	84	0	-1.0	55000	16665	16210		6.9	
				0.5	-1.0	55000	16540	16300		7.1	
				1.0	-1.0	55000	17380	16245		7.6	
	18	03	84	0	-1.0	52000	16638	16638		5.7	3.9
				0.5	-1.5	54000	17803	17135		3.8	4.2
				1.0	-1.5	55000	16850	15785		4.0	4.3
				1.5	-1.5	56500	17448	17078		3.8	4.3
	20	04	84	0	8.5	26500					8.5
				0.5	11.0	52000					
				1.0	11.0	56000					7.0
				1.5	8.5	60000					
	07	05	84	0	7.0	38000	8534	8370		0.1	7.6
				0.5	12.0	53000	16978	16320		0.2	4.8
				1.0	16.5	62000	18530	17943		0.7	4.3
				1.5	16.5	87000					
	14	05	84	0	12.5	39500					
				0.25	12.5	39500					
				0.5	12.5	39500					
				0.75	13.0	40000					
				1.0	19.0	58000					
				1.25	20.0	65000					
				1.5	21.0	72000					
	28	05	84	0	14.0	45000					
				0.25	14.0	45000					
				0.5	14.0	45000					
				0.75	14.0	45000					
				1.0	14.0	45000					
				1.25	16.0	52000					
				1.5	17.0	59000					
	11	06	84	0	14.5	49000	12728	11870	10295	0.7	5.5
				0.25	14.5	49000					
				0.5	14.5	49000	12450	12238	10355	2.6	5.3
				0.75	14.5	49000					
				1.0	14.0	49000	15570	15185	12765	1.0	4.4
				1.25	14.0	49000					
				1.5	15.5	65000					
	18	06	84	0	17.5	49500					
				0.25	17.5	50000					
				0.5	17.5	49500					
				0.75	17.5	50000					
				1.0	17.5	50000					

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				1.25	20.0	54000					
				1.5	20.5	70000					
	03	07	84	0	18.0	53000					
				0.25	18.0	53000					
				0.5	18.0	53000					
				0.75	18.0	53000					
				1.0	18.0	53000					
				1.25	18.0	53000					
				1.5	21.0	72000					
	16	07	84	0	20.0	56000	14315	14078	11338	2.8	5.5
				0.25	20.0	56000					
				0.5	20.0	56000	14608	13805	11415	3.6	5.5
				0.75	20.0	56000					
				1.0	20.0	56000	15821	15510	13165	2.4	3.2
				1.25	20.0	56000					
				1.5	21.0	70000					
	23	07	84	0	19.0	56000					6.7
				0.25	18.5	56000					
				0.5	18.5	56000					7.8
				0.75	18.5	56000					
				1.0	18.5	57000					3.1
				1.25	20.0	62000					
				1.5	22.0	79000					
	07	08	84	0	24.0	58000					
				0.25	24.0	59000					
				0.5	23.5	61000					
				0.75	23.5	61000					
				1.0	23.5	61000					
				1.25	24.0	64000					
				1.5	26.0	79000					
	20	08	84	0	18.5	61000					5.9
				0.25	18.5	61000					
				0.5	18.5	61000					4.9
				0.75	18.5	62000					
				1.0	18.5	62000					3.0
				1.25	22.0	72000					
				1.5	22.0	79000					
	27	08	84	0	19.5	64000	15383	15133	14550	2.5	4.9
				0.25	19.5	64500					
				0.5	19.5	65000	15755	14528	14750	2.7	4.9

Table E2 (continued)

Lake	D	M	Y	Depth	Temp	Cond	TP	TDP	SRP	Chl	DO
				0.75	19.5	65500					
				1.0	20.0	66000	15375	14830	14825	1.5	4.3
				1.25	22.0	74000					
				1.5	23.0	78000					

Table E3: ^{14}C primary productivity data for the three saline study lakes. Variables are defined as follows:

D = day
M = month
Y = year
Light = light bottle readings ($mgC\text{-}m^{-3}\text{-}h^{-1}$)
Dark = dark bottle readings ($mgC\text{-}m^{-3}\text{-}h^{-1}$)
L(kill) = formalin-killed light bottle readings ($mgC\text{-}m^{-3}\text{-}h^{-1}$)
D(kill) = formalin-killed dark bottle readings ($mgC\text{-}m^{-3}\text{-}h^{-1}$)

Lake	D	M	Y	Depth	Light	Dark	L(kill)	D(kill)
Fluevog	16	05	84	0.2	9	5		29
				0.5	4	3		
				1.0	9	4		
	20	06	84	0.2	68	65		65
				0.5	12	18		
				1.0	1	2		
				1.5	2	2		
	25	07	84	0.2	28	22		19
				0.5	42	32		
				1.0	44	43		
				1.5	58	47		
	22	08	84	0.2	55	56	42	52
				0.5	51	41	46	41
				1.0	59	62	33	51
Peninsula	15	05	84	0.2	23	7		8
				0.5	20	7		
				1.0	12	5		
				1.5	12	4		
	29	05	84	0.2	27	13		8
				0.5	36	11		
				1.0	12	10		
				1.5	14	15		
	19	06	84	0.2	58	59		51
				0.5	69	56		
				1.0	62	55		
				1.5	68	47		
				2.0	59	50		
	04	07	84	0.2	147	46		45
				0.5	48	64		
				1.0	49	95		
				1.5	28	49		
				2.0	121	119		
	24	07	84	0.2	30	21		21
				0.5	33	17		

Table E3 (continued)

Lake	D	M	Y	Depth	Light	Dark	L(kill)	D(kill)
				1.0	30	44		
				1.5	22	34		
				2.0	30	33		
	08	08	84	0.2	64	76		59
				0.5	75	18		
				1.0	61	30		
				1.5	68	99		
				2.0	252	108		
	21	08	84	0.2	68	55	46	38
				0.5	57	46	27	35
				1.0	58	27		29
				1.5	46	31		
Oliva	14	05	84	0.2	1869	2095		1788
				0.5	2315	115		
				1.0	124	97		
	28	05	84	0.0				1414
				0.2				1180
				0.5				1432
				1.0				1239
	18	06	84	0.2	541	579	485	515
				0.5	569	513	627	615
				1.0	601	577	574	579
	23	07	84	0.2	279	161		598
				0.5	305	176		
				1.0	591	303		
	07	08	84	0.2	503	564	435	240
				0.5	557	817	545	451
				1.0	1305	1913	1352	616
	20	08	84	0.2	1202	839		797
				0.5	1322	1146		
				1.0	958	1019		

Table E4: O_2 primary productivity data for Oliva Lake. Variables are defined as follows:

D = day
M = month
Y = year
Light = light bottle readings (mg O_2-L^{-1}-h^{-1})
Dark = dark bottle readings (mg O_2-L^{-1}-h^{-1})

Lake	D	M	Y	Depth	Light	Dark
Oliva	03	07	84	0.2	3.6	3.5
				0.5	3.4	3.5
				1.0	3.1	2.8
	23	07	84	0.2	1.7	1.8
				0.5	1.8	1.7
				1.0	0.9	1.1
	20	08	84	0.2	4.4	2.8
				0.5	4.1	3.1
				1.0	4.1	2.6

Table E5: Phytobenthos chlorophyll (Chl*a*) areal estimates in the three saline study lakes in two strata of sediment depth - shallow < 0.5 m and deep > 0.5 m. D = day, M = month, Y = year.

Lake	D	M	Y	Chl*a* ($mg \cdot m^{-2}$)	
				Shallow	Deep
Fluevog	30	05	84	24.8	17.3
	05	07	84	28.1	18.2
	09	08	84	5.2	22.2
Peninsula	29	05	84	26.1	5.3
	04	07	84	2.1	8.4
	08	08	84	6.9	37.2
Oliva	28	05	84	16.5	19.8
	03	07	84	2.8	91.56
	07	08	84	11.9	124.1

Table E6: Results of ^{32}P-PO_4 uptake experiments in the three saline study lakes. Variables are defined as follows:

D = day
M = month
Y = year
Time = duration of experiment (min)
$\%^{32}P$(beg) = $\%^{32}P$-PO_4 of total inoculum remaining in filtrate at beginning of experiment
$\%^{32}P$(end) = $\%^{32}P$-PO_4 of total inoculum remaining in filtrate at end of experiment

Lake	D	M	Y	Time	$\%^{32}P$(beg)	$\%^{32}P$(end)
Fluevog	18	07	83	180.97	97.6	97.7
				134.55	94.9	96.0
	05	08	83	4303.25	87.5	95.7
				4160.15	84.0	93.6
	30	05	83	313.00	98.0	97.6
				288.17	97.3	96.5
	05	07	84	317.17	98.0	97.7
				305.25	97.7	96.4
	09	08	84	328.33	99.8	92.4
				314.42	99.5	98.5
Peninsula	20	07	83	143.75	95.0	94.9
				122.39	95.6	96.1
	29	05	84	330.25	96.9	98.1
				313.50	97.3	97.7
	04	07	84	334.00	99.7	99.7
				321.17	98.6	97.4
	08	08	84	327.00	99.8	99.7
				315.17	98.2	99.3
Oliva	21	07	84	175.00	96.1	94.5
	28	05	84	331.50	96.9	97.9
				317.50	97.3	97.6
	03	07	84	321.00	99.8	99.7
				314.17	99.8	97.3
	07	08	84	307.33	99.8	97.9
				294.42	99.7	99.3

Table E7: 1984 bacterial densities in the three saline study lakes (counts by D. Bird, McGill Univ.). D =day, M = month, Y = year.

Lake	D	M	Y	Bacteria (10^6cells-mL^{-1})
Fluevog	30	05	84	10.7
	20	06	84	19.2
	16	07	84	9.9
	22	08	84	6.7
Peninsula	29	05	84	11.1
	17	06	84	11.5
	16	07	84	9.6
	21	08	84	19.3
Oliva	28	05	84	30.0
	18	06	84	32.5
	16	07	84	17.8
	20	08	84	19.1

Table E8: Chlorophyll (Chl*a*) levels in laboratory bioassay addition experiments. Chl*a* data given are means of 3 - 4 replicates ± the standard deviation. Variables are defined as follows:

Test = nutrients, ions or solutions added
(SE = soil extract)
Conc = final concentration in experimental flasks of added nutrients, ions or solutions
D = day
M = month
Y = year
Control = Chl*a* ($\mu g \cdot L^{-1}$) in control flask
Expt = Chl*a* ($\mu g \cdot L^{-1}$) in experimental flasks with added nutrients, ions or solutions

Test	Conc	Lake	D	M	Y	Control	Expt
KH_2PO_4	2 X lake	Fluevog	21	06	85	5.9 ±0.9	5.7 ±1.0
			21	06	85	5.9 ±0.9	5.9 ±0.4
		Peninsula	21	06	85	7.2 ±0.5	6.8 ±1.0
			21	06	85	7.2 ±1.5	6.9 ±0.5
		Oliva	21	06	85	19.0 ±1.5	21.7 ±2.9
			21	06	85	19.0 ±1.5	19.7 ±2.9
KNO_3	1.5 X lake	Fluevog	18	07	85	5.5 ±0.5	69.3 ±16.3[1]
			18	07	85	5.5 ±0.5	133.3 ±17.8[1]
		Peninsula	18	07	85	18.2 ±4.2	197.9 ±77.7[1]
			18	07	85	18.2 ±4.2	111.5±4.2[1]
		Oliva	18	07	85	22.2 ±1.5	190.2 ±60.4[1]
			18	07	85	22.2 ±1.5	189.9 ±70.5[1]
	2 X lake	Fluevog	28	05	85	13.8 ±2.0	52.3 ±13.8[1]
			21	06	85	5.9 ±0.9	70.8 ±5.9[1]
		Peninsula	16	07	84	24.0 ±0.7	175.4 ±25.2[1]
			21	06	85	7.0 ±1.4	63.4 ±9.7[1]
		Oliva	01	06	85	29.6 ±2.6	121.5 ±3.1[1]
			21	06	85	19.0 ±1.5	111.7 ±3.5[1]
	4 X lake	Fluevog	28	05	85	13.8 ±2.0	119.5 ±28.1[1]
			21	06	85	5.9 ±0.9	209.9 ±8.5[1]
		Peninsula	16	07	84	24.0 ±0.7	207.8 ±69.5[1]
			21	06	85	7.0 ±1.4	271.5 ±57.6[1]
		Oliva	01	06	85	29.6 ±2.6	91.5 ±22.0[1]
			21	06	85	19.0 ±1.5	276.4 ±68.2[1]
NH_4Cl	1.5 X lake	Fluevog	18	07	85	5.5 ±0.5	46.9 ±22.6[1]
			18	07	85	5.5 ±0.5	44.5 ±7.8[1]
		Peninsula	18	07	85	18.2 ±4.2	54.4 ±6.5[1]
			18	07	85	18.2 ±4.2	27.4 ±4.0[1]

Table E8 (continued)

Test	Conc	Lake	D	M	Y	Control	Expt
		Oliva	18	07	85	22.2 ±1.5	70.8 ±17.0[1]
			18	07	85	22.2 ±1.5	96.7 ±7.3[1]
	2 X lake	Fluevog	28	05	85	13.8 ±2.0	39.6 ±8.4[1]
			21	06	85	5.9 ±0.9	70.5 ±6.36[1]
		Peninsula	16	07	84	24.0 ±0.7	164.9 ±43.3[1]
			21	06	85	7.0 ±1.4	73.3 ±0.7[1]
		Oliva	01	06	85	29.6 ±2.6	111.7 ±14.4[1]
			21	06	85	19.0 ±1.5	111.8 ±3.0[1]
	4 X lake	Fluevog	28	05	85	13.8 ±2.0	37.3 ±14.9[1]
			21	06	85	5.9 ±0.9	5.8 ±5.5
		Peninsula	16	07	84	24.0 ±0.7	316.5 ±93.0[1]
			21	06	85	7.0 ±1.4	215.9 ±30.0[1]
		Oliva	01	06	85	29.6 ±2.6	79.8 ±83.3[1]
			21	06	85	19.0 ±1.5	200.5 ±57.8[1]
SE	20mL-L^{-1}	Fluevog	30	10	83	5.4 ±0.7	5.4 ±1.5
			01	06	85	7.2 ±1.0	8.2 ±1.3
		Peninsula	06	07	84	13.8 ±5.3	20.2 ±4.7
			01	06	85	6.0 ±0.5	5.3 ±1.0
		Oliva	30	10	83	24.4 ±3.3	28.8 ±0.5
			01	06	85	30.2 ±4.0	29.0 ±16.0
EDTA	0.2mM	Fluevog	30	10	83	5.4 ±0.7	5.4 ±1.3
			01	06	85	7.2 ±1.0	5.4 ±1.5
		Peninsula	06	07	84	13.8 ±5.3	19.6 ±2.6
			01	06	85	6.0 ±0.5	7.9 ±2.2
		Oliva	30	10	83	24.4 ±3.3	35.8 ±4.8[1]
			01	06	85	30.3 ±4.0	37.0 ±6.0[1]
	0.4mM	Fluevog	18	07	85	5.5 ±0.5	5.7 ±2.1
			18	07	85	5.5 ±0.5	6.7 ±0.7
		Peninsula	18	07	85	18.2 ±4.2	19.7 ±3.7
			18	07	85	18.2 ±4.2	19.2 ±1.8
		Oliva	18	07	85	22.2 ±1.5	43.65 ±6.04[1]
			18	07	85	22.2 ±1.5	34.8 ±8.8[1]

[1] = Chl*a* levels that differ significantly ($P < 0.05$) from control levels.

Table E9: Comparison of chlorophyll (Chl*a*) levels in 100 mL flasks (*in situ*) with and without grazing zooplankton. Density of grazers comparable to lake densities at the time of the experiments. Chl*a* data given are means of 2 replicates ± the standard deviation. Variables are defined as follows: —

D = day
M = month
Y = year
Time = duration of experiment (h)
Depth = depth of experiment in lake (m)
Control = Chl*a* ($\mu g \cdot L^{-1}$) in control flasks without grazers
Grazed = Chl*a* ($\mu g \cdot L^{-1}$) in experimental flasks with grazers

Lake	D	M	Y	Time	Depth	Control	Grazed
Fluevog	05	07	84	2.0	0.2	4.2 ±0.2	4.5 ±0.3
	09	08	84	2.0	0.2	4.0 ±0.7	3.4 ±0.8
Oliva	03	07	84	2.0	0.2	1.1 ±0.1	2.1 ±0.2
	07	08	84	2.0	0.2	1.5 ±0.1	2.9 ±0.5

Table E10: Zooplankton species counts–per L for the three saline study lakes. Variables are defined as follows:

D = day
M = month
Y = year
D.sim = *Daphnis similis* Leach
naup1 = *D. similis* nauplii
D.nev = *Diaptomus nevadensis* Light
D.sic = *Diaptomus sicilis* Forbes
coped = copepodites for both *Diaptomus* spp.
naup2 = nauplii for both *Diaptomus* spp.
Artem = *Artemia salina* Leach
naup3 = *Artemia* nauplii
B.plic = *Brachionus plicatilis* Muller
Hex = *Hexarthra* spp.

Table E10 (continued)

Lake	D	M	Y	D.sim	naup1	D.nev	D.sic	coped	naup2	Artem	naup3	B.plic	Hex
Fluevog													
	20	04	84	0.33	0.07	0.05	11.21	43.82	9.85				
	07	05	84	26.67	6.67	4.08	27.50	12.92	0				
	16	05	84	20.83	3.75	1.57	21.67	12.08	0				
	30	05	84	13.89	1.67	1.97	12.22	6.39	0				
	11	06	84	19.83	1.33	1.64	8.34	8.50	0				
	20	06	84	6.01	0.57	1.95	6.88	6.13	0.06				
	05	07	84	1.12	0.04	1.28	8.38	10.83	0.96				
	25	07	84	11.63	0.75	0.79	22.46	21.00	6.56				
	09	08	84	10.84	1.67	0.37	26.34	12.17	1.84				
	27	08	84	20.50	0.21	1.07	41.50	3.99	3.75				
Peninsula													
	20	04	84	0.50	0.04	0.04	2.10	2.50	11.05				
	07	05	84	22.29	2.08	0.87	10.83	9.17	19.38				
	15	05	84	23.43	0.06	0.52	10.94	15.62	18.75				
	29	05	84	32.92	2.08	0.59	17.08	15.83	4.17				
	11	06	84	12.28	0.73	0.78	13.37	19.20	0.61				
	19	06	84	16.25	0.88	0.99	16.00	27.25	4.25				
	04	07	84	6.67	0.83	0.49	28.55	23.75	5.30				
	24	07	84	20.27	2.63	0.29	29.31	18.96	2.48				
	08	08	84	10.88	1.88	0.45	34.88	5.88	1.38				
	27	08	84	25.00	0	0.42	50.00	9.25	4.50				
Oliva													
	20	04	84							0	79.17	0	0
	07	05	84							25.21	1.79	0	0
	14	05	84							49.69	2.81	5.62	0
	28	05	84							19.50	0.86	0	0
	11	06	84							17.81	0.29	0	0.29
	18	06	84							18.10	0.47	11.16	15.09
	03	07	84							3.30	0	3.75	1828.
	23	07	84							2.50	0	0.14	1606.
	07	08	84							0.82	5.73	76.25	1470.
	27	08	84							4.35	3.19	4.38	45.16